THE DYNAMICS OF HERBAGE PRODUCTION AND UTILISATION IN SWARDS GRAZED BY CATTLE AND SHEEP

Julio Cesar Arosteguy

Ph.D.

University of Edinburgh

1982

ACKNOWLEDGEMENTS

This study was made possible in part by the awarding of a two year fellowship of Consejo Nacional de Investigaciones Cientificas y Tecnologicas, and a one-year fellowship of Instituto Nacional de Tecnologia Agropecuaria, both from Republica Argentina. The experimental work was carried out at the Glensaugh and Hartwood Research Stations of the Hill Farming Research Organisation.

I wish to thank the Director of the Hill Farming Research Organisation, Mr J. Eadie, and his predecessor, Professor J.M.M. Cunningham, for permission to undertake this study and for providing facilities at the Institute.

I am deeply grateful to Dr J. Hodgson for his help and guidance during the development of the project. I am very appreciative of having received much of his time for discussion, and his constructive criticism and helpful suggestions for the preparation of the manuscript.

I wish to thank Dr A. Illius, of the School of Agriculture, of the University of Edinburgh and Dr J. King and Miss S.A. Grant of H.F.R.O. for their helpful criticism of the manuscript.

In addition I wish to thank Mr R. Thompson for help and advice with the statistical analyses and Miss H. Smith for useful discussion on statistical methods. Mr A. Sibbald, Dr J. Rogers, Miss E.V. Deans and Mrs H. Talbot of the E.R.C.C. helped me to acquire the necessary computing skills to develop the project.

I am grateful to Dr J.S. Bircham for helpful discussions at the initial stages of the project, and for the use of his

program for handling the field records.

Mr C.C. Evans and his staff did the faecal chromium analyses and Mr D.R. Campbell and his staff did the *in vitro* digestibility analyses. Sincere thanks are extended to the following persons for extensive help with field work. Without their help the project would not have been possible.
Mr W.G. Souter, Mr G.T. Barthram, Miss L. Torvell, Miss R. Wilson, Miss A. Mark, Dr J.S. Bircham, Mr G. King, Mr M.M. Beattie, Mr R.H. Armstrong, Miss V.A. Doughty, Mrs E.M. Sim and Mr D. Sinclair.

Thanks for assistance in field and laboratory measurements are also due to Miss C. Williams, Mr T.G. Common, Dr J. Hodgson, Dr A. Illius, Miss L. Waterfield, Mr D.E. Suckling and Mr D. Havranek.

Mr I.R. Pitkethly prepared the figures and the photographic work.

Mrs E.B.H. Reid and Mrs M. Purves for typing the drafts, Mrs J.P. Mabon for typing the drafts and the final manuscript and Mrs M.J. Williamson for collaboration in the final preparation of this work.

I wish to thank Dr T.D.A. Forbes for many stimulating discussions and Mr A. Huber for allowing me to use unpublished work.

I wish to thank the Scottish people for the friendship offered to me and my family and for the opportunity given to us of enjoying their way of life. I am particularly indebted to the staff of H.F.R.O. for the moral and material support they have given to me when unfortunate decisions put both countries in war.

Finally I wish to thank Graciela for much help given during the development of the project, and I wish to thank her and our children Julieta and Agustin for giving up their demands on my time and tolerating me for these last 33 months.

ABSTRACT

THE DYNAMICS OF HERBAGE PRODUCTION AND UTILISATION IN SWARDS GRAZED BY CATTLE AND SHEEP

J.C. Arosteguy University of Edinburgh

There is limited evidence to suggest that the rate of net herbage accumulation is greater on swards grazed by sheep than on those grazed by cattle. However, the evidence is not unequivocal and in some cases the effect of animal species and of grazing pressure appears to be confounded.

Two field experiments were conducted on mixed species (*Lolium perenne* L, *Poa annua* L and *Trifolium repens L)* swards to examine the effects of cattle and sheep grazing alone or in combination on plant tissue and tiller turnover. Established swards of perennial ryegrass and white clover with variable content of *Poa annua* were continuously stocked from May to September with either sheep or cattle or a combination of both. Animal numbers were adjusted frequently to maintain sward surface height as near steady state as possible.

In the first experiment swards grazed by ewes and lambs or by yearling female cattle were compared. The swards were maintained at sward surface height of 2.0-2.5 and 3.0-3.5 cm (sheep), and 2.0-2.5, 3.0-3.5 and 6.0-6.5 cm (cattle), equivalent to herbage mass of 1700, 2100 and 3100 kg ha^{-1}.OM. Estimates of the rates of herbage growth, senescence and net production (growth minus senescence) were derived from measurements on individually identified tillers and clover active meristematic points on three occasions during the season.

Tiller populations were lower on cattle-grazed than on comparable sheep-grazed swards, and this was largely due to high rate of tiller disappearance on cattle-grazed swards. The differences in tiller density were in turn responsible for differences in growth and net production rate.

There were seasonal differences in the botanical composition of the diet selected by cattle and sheep, and these differences were reflected in the higher digestibility of the diets selected by sheep.

The herbage intake of both cattle and sheep increased with the level of herbage mass maintained and sheep spent more time grazing than cattle. At the lower herbage mass sheep appeared to be better able to maintain rate of intake than cattle. There were similar proportions of under-grazed herbage on the plots grazed by the two species, although undergrazed areas on cattle swards were taller than those on sheep swards.

In the second experiment, swards continuously stocked by wether sheep or yearling cattle, singly or in combination, were maintained at sward surface height *ca.* 3.0 and 4.5 cm equivalent to herbage masses of 1600 and 1900 kg ha^{-1}.OM. Similar observations as in the first experiment were made.

Tiller density in cattle-stocked swards was lower than in the mixed- and sheep-stocked swards, and observations confirmed higher rates of tiller disappearance under cattle grazing. The effect of the reduced tiller density on herbage growth and net production rates was partially confirmed. Sheep grazed alone or in combination selected diets with higher lamina proportion than cattle and the proportion of lamina selected by both animal species was lower when

grazing in combination than when grazing alone. The proportion of the area left under-grazed was similar for the two species grazing alone and in combination. It is concluded that tiller density has a direct effect on the stability in the rate of herbage production, and that competitive rather than complementary grazing activities, are likely under intensive mixed-stocking systems.

In addition two greenhouse experiments were carried out to examine the effect of controlled defoliation under sward-like conditions on tiller growth and development. The principal interest was on leaf extension rates and tiller associations but from the observations made, it was possible to conclude that errors in the estimation of tissue fluxes using conventional field techniques are likely to be relatively small.

CONTENTS

LIST OF PLATES

CHAPTER 1

INTRODUCTION

Grazing is the most primitive system of transforming plant into animal tissue, and grazing management has been the subject of investigation for many years. However there is still much controversy regarding the merits of different management systems. This is hardly surprising since the cyclic interactions between the animal and its food can make difficult the interpretation of the results of grazing experiments. The objective of management is to achieve efficiency in the conversion of organic matter formed by the sward into profitable forms of animal tissue, compatible with the conservation of plant resources. Two areas of knowledge are necessary to an objective evaluation of the scope for management manipulation. The first is a quantitative understanding of the organic matter fluxes under grazing, and the second is a detailed knowledge of the relationship between the animal and its pasture. It has been recently shown that the rate of net herbage production is little affected by differences in herbage mass or leaf area (Hodgson *et al*, 1981) because the turnover of organic matter and of tillers serve to buffer the impact of management variations.

Detailed studies of tissue flow and of the relationship between animal species and their pasture has been carried out in most of the cases with sheep. However, the different grazing habits of sheep and cattle (Arnold and Dudzinski, 1978; Van Dyne *et al*, 1980) may create differences in sward population and structure which in turn may affect the dynamics of growth and senescence. If grazing systems are to become specialised, it will be necessary to distinguish between swards suitable for cattle and swards suitable for sheep. There is some evidence that animal output is higher from non-specialised systems (i.e. mixed grazing of cattle and sheep) than

from specialised ones (Nolan and Connolly, 1977), but the nature of the mechanisms generated by the mix of species are still unknown and, before examining the influence of mixtures of cattle and sheep in herbage dynamics, a better understanding of the structure and function of the single-species systems seems to be the best approach (Hodgson and Forbes, 1980; Eadie, 1981).

The objective of the project described here was to investigate the dynamics of growth and utilisation in swards grazed by cattle and by sheep. To facilitate this a continuous stocking management was adopted and animal numbers were manipulated to maintain swards approximately under steady state (Hodgson *et al*, 1981).

Two field experiments were conducted to study the patterns of tissue flow, one under single-species grazing (cattle or sheep) and the other under single-compared with combined-species grazing.

Two additional greenhouse experiments were conducted to study the effect of controlled defoliation under sward-like conditions on tiller growth and development and the results were used to discuss some assumptions made in the techniques applied.

CHAPTER 2

REVIEW OF LITERATURE

INTRODUCTION

The purpose of this review is to consider the published evidence on the grazing habits of cattle and sheep, and their effects on sward characteristics and herbage production. The physiology of growth and senescence are not considered since comprehensive reviews on different aspects of the subject have been recently published (Silsbury, 1970; Hodgson *et al*, 1981; Robson, 1981; Vickery, 1981). After a brief discussion of mixed stocking in agriculture, a review of herbage production, tiller population dynamics, grazing efficiency and herbage intake in relation to mixed stocking systems is presented.

MIXED STOCKING IN AGRICULTURE

Mixed stocking systems have been used in agriculture for many years. Man possibly copied them from nature where a number of species generally co-occur in the same environment. The mechanisms which permit the species to co-exist may be seen as reduced competition between species which fill different niches. Harper (1967) suggested that species avoiding competition become niche specialised and this brings stability and diversity into ecosystems. These theories lead to the logical conclusion that complex ecosystems are more efficient than simple ones in using the environmental resources.

The African Savannah (Bell, 1970), in the Serengeti National Park, has been taken as one example where a high diversity of ungulates co-graze a series of plant communities during their seasonal movements. It has been suggested that complementarity in using plant resources (i.e. some species modify the vegetation for the next species in the catena) and different degrees of specialisation in diet selection, associated with migration capacity are all of importance in this system (Bell, 1970; Van Dyne *et al*, 1980).

Under extensive agriculture in the Scottish hills, Peart (1963) attributed higher production in mixed stocked systems to a complementary use of the vegetation by suckling cows and ewes.

As a generalisation, it might be suggested that when diversity exists, and competition between species is low, a complementary use of vegetation may be operative. Although this generalisation is supported only by theoretical speculation, it may reasonably explain some of the published work claiming higher production by mixing animal species. However, modern agriculture is characterised by low diversity, as a consequence of managing the physical environment and the biological components of production systems (Snaydon, 1980). In this context, different animal species grazing on relatively simple swards and with restricted amounts of herbage on offer may find less opportunities for complementary use of the vegetation (Hodgson and Forbes, 1980).

Agricultural experimentation on mixed grazing has been mainly restricted to associations of cattle with sheep and the published work has been reviewed by Nolan and Connolly (1977). They conclude that output of animal product per unit area of grassland is usually higher under mixed grazing than under single species grazing, and discuss the factors which are likely to explain this effect.

There are managerial and profitability reasons to run mixed enterprises. Managing more than one kind of livestock may give some flexibility to the system if labour, fencing, water and buildings can be used complementarily. Furthermore, the mixed enterprise may be financially more stable than either single enterprise, by buffering

the effects of fluctuation in prices for beef, wool and sheep meats (Morley, 1981).

Any production advantages to mixed stocking managements may be attributed to one or a combination of several of the following variables (Table R1).

Table R1. Reasons suggested as being responsible for some of the advantages found in mixed grazing compared with single species grazing (Nolan and Connolly, 1977; Hodgson and Forbes, 1980).

1. Epidemiological
2. Herbage production
3. Herbage intake
4. Grazing efficiency (total intake of the animal populations % gross growth)
5. Complementarity in seasonal patterns of nutritional requirements
6. Differential sensitivity to nutritional limitations

There is epidemiological justification for mixed grazing, related mainly to helminth parasites. If different animal species are grazed together the stocking rate of each host species, and hence the level of contamination by each parasite species, must be decreased (Black, 1980; Morley and Donald, 1980). The use of a mix of sheep and cattle to reduce parasite infestation of pastures, and its managerial limitations, have been recently reviewed by Morley and Donald (1980). Other reasons have been quoted as likely to contribute to a higher production by mixing stock, such as complementarity in seasonal patterns of nutrient requirements and differential sensitivity to nutritional limitations. Although

these advantages seem very likely to occur, they are system advantages rather than fundamental differences.

A higher growth of herbage, increased intake by the animal population and a more even utilisation of the herbage grown or combinations of these have been quoted as possible explanations for the higher levels of production on mixed stocked systems (Nolan and Connolly, 1977; Hodgson and Forbes, 1980; Nolan, 1980). However, the evidence is not unequivocal and in some cases the effect of animal species and grazing pressure appear to be confounded (Reynolds *et al*, 1971; Connolly and Nolan, 1976; Brelim, 1979; Connolly, 1980). Most of the reported work in mixed grazing has been conceptually based on equalisation of grazing pressure, using livestock equivalents (Nolan and Connolly, 1977). Equalisation of grazing pressure of the mixed stock to that of the single species may be difficult because of the inadequacy of the existing tabulations of livestock equivalents (Connolly and Nolan, 1976). Different parameters have been involved in calculating livestock equivalents, such as total digestible nutrient intake (Clark, 1963), estimated voluntary intake of pastures with the same organic matter digestibility (Conway, 1973), ratios of metabolic body weights (Attwood and Heavey, 1964; Graham, 1972), relationship between dry matter intake and animal weight (Baker, 1964). However no one of these systems includes elements of animal performance and stocking rate, and in practice actual intake often is different from that estimated from tables. Connolly and Nolan (1977) and Connolly (1980) suggest an approach appropriate to mixed grazing experiments, in which equivalents are calculated restrospectively on the basis of the results obtained.

However, if this information is to be used in decision making, it should be available *a priori*, i.e. the equivalents should be predicted and not determined.

The use of treatments involving strict control of specified sward conditions may help to avoid the livestock equivalents difficulties. Hodgson and Forbes (1980) discussed the variables involved in the dynamics of herbage growth and utilisation (see items 2, 3 and 4 of Table R1) and their relevance in mixed stock studies. They concluded that a better understanding of tissue flow (i.e. growth, senescence and intake) and grazing efficiency (i.e. growth - consumption ratio) under single species grazing is necessary to interpret the results from mixed stocking experiments. The remainder of this chapter is devoted to a review of the factors that influence tissue flow in grazed swards and the sensitivity of these factors to different species grazing. Thus herbage production, tiller appearance and disappearance and its effects on net production, intake per animal and diet selection as determinants of grazing efficiency are considered. The terminology suggested by Hodgson (1979) and by Thomas (1980) for detailed grazing and grassland studies is used.

HERBAGE PRODUCTION

Herbage production is measured in grazing experiments as the net accumulated balance between the rates of growth and senescence between two sets of measurements (Hodgson and Wade, 1978). The rate at which herbage is produced in a sward protected from defoliation (NP) may be expressed as the difference between the rate of growth of new tissue (G) and the rate of loss of mature tissue to decomposition: (D)

$$NP = G - D \qquad \text{e.q. R.1}$$

When the animal is present, the net accumulation of herbage (NHA) is a function of growth, losses to decomposition, and consumption (C) (Bircham, 1980; Bircham and Hodgson, 1981; Hodgson *et al*, 1981).

$$NHA = G - (D + C) \qquad \text{e.q. R.2}$$

From equation R.2 it can be seen that, if NHA is equal to zero, the tissue that is not consumed goes to the decomposition pathway. Failure to consider these aspects has led to difficulties in interpretation of the experimental results on defoliation strategies either under cutting or grazing regimes (Hodgson *et al*, 1981).

Net herbage production has been reported to be substantially greater under sheep than under beef cattle grazing (Monteath *et al*, 1977; Boswell, 1978) although the reverse has also been reported (Joyce, 1970). On the other hand, Boswell and Cranshaw (1978) found no differences in net herbage production between cattle- and sheep-grazed paddocks, but they did find higher net production in swards grazed by cattle and sheep together. Since experimental conditions were not strictly comparable between experiments, the results must be interpreted separately. Monteath *et al*, (1977) managed cattle swards at a taller residual height than sheep swards, and most of the residual herbage mass must have gone to the senescence and decomposition pathway (see e.q. R.2). Therefore, lower net herbage production may have been the result of higher losses rather than differences in growth rate. Bircham (1980) has emphasised the importance of equalised utilisation across treatments in the interpretation of results from grazing experiments.

Boswell (1978) managed swards at the same height under cattle and sheep grazing and he attributed the lower net production in cattle swards to a reduced number of tillers as a consequence of cattle pulling them off. The turnover of tillers (Jones and Mott, 1980) may only be detected if detailed studies are conducted, this fact highlights the difficulty in the interpretation of grazing experiment results when only gross variables such as herbage mass are recorded. This concept is supported by the view of Davies (1977) and Hodgson (1981a) who suggested that swards should be studied as associations of individual plant units rather than as an amorphous collection of foliage or biomass.

TILLER POPULATION DYNAMICS IN GRAZED SWARDS

Population density as it is usually evaluated, is the accumulated net result of both recruitment and death of individual plants (Harper, 1977). Sward populations are dynamic entities in either stable or unstable (positive or negative) equilibrium, depending on the relative magnitude of the two rates. Management has been shown to affect tiller density and net changes can be extremely rapid, often over short periods of time. Bircham (1981a) was able to reduce tiller numbers by 25% over a period of three weeks by changing herbage mass from 1700-2100 kg ha^{-1} to 700-1000 kg ha^{-1}. However, positive changes seem to be slower, since the reverse treatment resulted in little change in the number of tillers per unit area. It has been shown that, under grazing, intermediate levels of defoliation produce the more dense swards, while both severe and lax defoliation produce less densely populated swards (Brougham, 1959; Bircham and Hodgson, 1981; Smith *et al*, 1971b). On the other hand, Hodgson and Wade (1978) showed that swards under continuous grazing had higher tiller populations than

swards under rotational grazing. The species of grazing animal seem to affect number of tillers per unit of area, cattle producing less dense swards than sheep (Mitchell and Glenday, 1958; Monteath et al, 1977; Boswell and Crawford,1978; Briseno de la Hoz and Wilman,1981). The seasonal pattern of tiller densities seems to be little affected by grazing management (Tallowin, 1981) , although both seasonal and treatment effects seem to be confounded (Grant *et al*, 1981b). Despite the range of treatment effects upon tiller numbers, very little is known about management effects on tiller natality and mortality rates.

Tiller Natality

The rate of tiller appearance is initially the same as leaf appearance, since each leaf has the potential to develop its axillary bud. Under favourable conditions most of the buds become visible tillers, so the rate of tillering soon becomes exponential if environment is maintained constant (Davies, 1977; Langer, 1979). Although genotypic differences exist, tillering is highly modified by the light and nutrient environments (Langer, 1963; Davies, 1977; Langer, 1979). Low levels of nitrogen may lead to the cessation of tiller production (Cooper, 1951; Troughton, 1955) and in many swards this must be a major factor restricting tiller numbers. Grazing animals collect plant nutrients from a pasture and relocate a proportion of them in faeces and urine in greatly concentrated mass (Barrow, 1967). This redistribution of nutrients may create areas of variable size, depending on the pattern of faeces distribution of the species grazing (Petersen,Lucas and Woodhouse, 1956; Hilder, 1966), which enjoy high fertility levels, while other parts of the sward may become impoverished. Scott (1977) found that available soil N levels were lower under cattle-grazed than under

sheep-grazed paddocks in the experiment of Monteath *et al* (1977), but this result may be confounded with a presumably lower grazing pressure in the cattle paddocks. Absence of defoliation or lax defoliation may produce self shading of the tiller bases, reducing the rate of new buds development (Mitchell and Coles, 1955; Langer, 1979). However, severe defoliation may also reduce tiller production; Davies (1974) was able to prevent 50% of the available tiller buds from developing into visible tillers by removing all the leaf blades from experimental tiller populations.

Tiller Mortality

Causes of tiller death may be due to predation by small or large herbivores or to physiological reasons. In cereals and grasses, tiller death may occur at any time of the year, but high mortality has been reported to coincide with reproductive growth (Langer *et al*, 1964; Mathews and Westlake, 1969; Hill and Watkins, 1975; Bernard, 1976). The tiller mortality which is coincident with the time of stem elongation or ear emergence in other tillers which do not die, has been explained by the effect of competition from older flowering tillers for nutrients and assimilates (Langer, 1959). However, tiller mortality has also been described in vegetative swards by Kays and Harper (1974), who suggested that mutual self-shading may be responsible for plant and tiller mortality in the sward. Ong (1978) has shown that tiller death can be induced on a vegetative ryegrass plant by subjecting the whole plant to either nutrient stress, low light intensity or both, and that tillers which died were the smallest and often the youngest on the plant. However, tiller death may be delayed up to 60 days if the rest of the plant is maintained in a favourable light environment (Ong and

Marshall, 1979).

Ong *et al* (1978) found that the major causes of tiller death in a sward during undisturbed growth were physiological in origin associated with the failure of flowering tillers to support the growth of the young vegetative tillers, which are dependent on imported assimilate, nutrients and water for their growth and survival.

Mortality by predation

Herbage species are structurally adapted to varying degrees of defoliation and treading, but changes in botanical composition have been described in swards grazed either by sheep or by cattle (Jones, 1933a, b, c, d; Norman, 1957; Kydd, 1964, 1966). These changes have been interpreted in terms both of the competitive interaction between species and of the selectivity of the grazing animal. As grazing intensity increases, some other grazing effects become obvious. Treading can directly bruise or destroy growing points, stems and roots, and the animals may uproot entire plants or tillers. In this way herbage production may be affected, in the short term because regrowth is reduced, and in the long term because botanical changes may occur (Edmond, 1966).

The harvesting procedure developed by cattle, in which the tongue is rolled round a bunch of grass which is then pulled up, is likely to produce more uprooting compared with the biting action developed by sheep in which herbage is gripped between the incisor teeth and the dental pad before being severed. If the plant is well rooted the leaves break while being pulled up, but some plants may be physically uprooted by such a tearing action. The fact that defoliation reduces root weight (Schuster, 1964; Davidson, 1969; Evans, 1973), and that the leaves of different ages and species have

differential tensile strength (Evans, 1964, 1967a, b) may facilitate differential uprooting in different plant species. Pineiro and Harris (1978) found that tiller uprooting in ryegrass swards was negligible compared with *Bromus catharticus* swards grazed by sheep. *Agrostis stolonifera* (Harper, 1977) and *Poa annua* (Wells, 1974) have been quoted as sensitive to removal of whole group of weakly rooted tillers mainly when grazed by cattle. S.A. Grant (personal communication) has observed a high frequency of uprooting of *Poa annua* tillers in *Lolium perenne* dominant swards grazed by sheep, often associated with drought periods. Monteath *et al* (1977) and Boswell (1978) pointed out that, although higher physical uprooting of ryegrass tillers is apparent even in sheep pastures at dry periods, the incidence of uprooting is far higher under cattle grazing than under sheep grazing. They suggest that the higher tensile strength of ryegrass leaves (Evans, 1964, 1967a, b) under the pulling action of grazing by cattle means that often the break point of the tillers is at the root level.

Treading effects

Treading usually produces a significant and progressive reduction in net production of temperate pastures as stocking rate increases (Edmond, 1958, 1964, 1966, 1970). Both sheep and cattle cause treading damage, and the magnitude of the effect depends slightly on soil type and fertility, is moderately affected by sward height and strongly affected by plant species and soil moisture content (Edmond, 1970). Tiller density declines with treading intensity but reduction in tiller vigour is less marked (Edmond, 1958).

The static hoof load is markedly different in cattle and sheep, being 1.2-1.6 and 0.74-0.95 kg cm^{-2} respectively (Spedding,

1971; Frame, 1976) but their treading effects on swards are surprisingly similar (Edmond, 1970). However, Edmonds' techniques, involving high intensity and short duration of the treading may be somewhat artificial and considerably different from the treading experienced under farm conditions (Brown and Evans, 1973). A better understanding of the long term treading effects on tiller numbers is clearly necessary, but it is not easy to measure this effect except in artificial situations.

HOMEOSTASIS OF THE GRAZED SWARD

There is apparently little scope for modifying the net herbage production of continuously sheep stocked temperate swards by different defoliation strategies. Bircham and Hodgson (1981) and Hodgson *et al* (1981), have shown that defoliation strategies designed to create differences in LAI had only limited impact on the herbage net production over a range from 2-5 LAI units. Phenotypic plasticity at the plant unit level seems to compensate the effects on the population created by management strategies and, as a consequence, net production rate remained stable for a range of treatments at least in the short term. The self regulatory properties described for a range of woody and herbaceous species allowed to grow undisturbed (Yoda *et al*, 1963; White and Harper, 1970; Kays and Harper, 1974) also seem to be operational in grazed swards (Hodgson *et al*, 1981). In sheep-grazed swards, the net rate of herbage production seems to be stable in swards with a range of herbage mass from 1000 to 2000 kg DM ha^{-1}. Stability is lost below 700 kg OM ha^{-1} presumably because the self-regulatory mechanisms break down (Bircham and Hodgson, 1981; Hodgson *et al*, 1981). Cattle-grazed swards may operate in the same fashion but,

due to the lower number of tillers at comparable herbage mass (Boswell and Crawford, 1978; Briseno de la Hoz and Wilman, 1981), stability may break down at comparatively higher levels of herbage mass. In the long term, if the loss of tillers is cumulative, stability may be broken down by changes in botanical composition where the net accumulation rate of the coloniser species is lower than that of the originally sown species.

GRAZING EFFICIENCY

Many researchers attributed the benefits brought about by mixed stocking to the complementary grazing behaviour patterns of different animal species (Snell, 1935; Van Keuren and Parker, 1967; Peart, 1963; Hamilton, 1980; Nolan, 1980). Selection patterns may operate at two levels, one related to the choice of the grazing site and the other related to the bite selection, both levels being strongly affected by grazing pressure (Milne *et al*, 1979). Complementary patterns of diet selection may exist if both species do not overlap site and/or bite choice. In the natural Savannah (Bell, 1970), competition between species seems to be reduced by animals filling different food niches, animal size being a determinant of niche specialisation. However, Schwartz and Ellis (1981) found that dietary selectivity and diet overlap seemed to be dependent upon recent evolutionary history as well as upon body size, and upon forage quantity. They calculated a diet similarity coefficient (Morisita, 1959, modified by Horn, 1966) and showed almost complete overlap in the composition of diets selected by cattle and sheep throughout the year. Similarity between preference patterns of sheep and cattle grazing indigenous vegetation has also been reported by Grant and Hodgson (1980) and Hodgson and Grant (1981), although

Table R.2. Similarity coefficients (Morisita, 1959 as modified by Horn, 1966) from cattle and sheep diet composition estimated from Dudzinski and Arnold, 1973.

Trial No.	1	2	3	4	5	6	7	8	9	10	12	13	14	16	17	18
Trial date	Nov.	beg Dec	end Dec	beg Jan	mid Jan	mid Feb	beg Mar	beg Apr	beg May	mid June	end June	end Oct	end Oct	mid Dec	beg Jan	beg Feb
Herbage mass g m^{-2}	187	286	150	252	264	258	202	148	80	37	278	323	384	440	260	148
Similarity coefficient $C\lambda$ *	0.6	1.0	1.0	1.0	1.0	0.9	1.0	0.9	1.0	0.9	0.9	1.0	1.0	1.0	1.0	0.9

*Coefficient $C\lambda$ varies over the range from 0, for completely distinct samples (no species in common), to 1, for identical samples: $C\lambda = 2\sum_{i=1}^{s} xi\ yi / \sum_{i=1}^{s} xi^2 + \sum_{i=1}^{s} yi^2$. s is the total number of plant species and xi and yi are the proportion of the total diet of the herbivore species, x and y, taken from plant species i.

sheep diets contained higher proportions of the preferred components.

In tall indigenous swards, cattle appear to graze the upper horizons and sheep penetrate near the base of the sward (Grant and Hodgson, 1980; Hodgson and Grant, 1981; Forbes, 1982). This may be regarded as some degree of complementarity in grazing activity, in the sense that cattle grazing the sward surface may facilitate access for sheep to the lower horizons. In intensively grazed sown swards, dietary differences seem to be minimal (Hodgson and Forbes, 1980). However, differences in diet composition between sheep and cattle grazing sown swards under different intensities have been reported (Dudzinski and Arnold, 1973). Notwithstanding, when similarity coefficients (Morisita, 1959; Horn, 1966; MacArthur and Levins, 1966; Schwartz and Ellis, 1981) are calculated, almost complete overlap in diet composition can be shown (Table R.2). The coefficients shown in Table R.2, calculated for sown swards, tend to be higher than those calculated by Schwartz and Ellis (1981) for more diverse vegetation. Schwartz and Ellis (1981) suggest that sheep husbandry has caused sheep to lose their theoretical food specialisation so that their selective behaviour is now similar to that of cattle. Thus it is also likely that differences in selection capacity are lost because grazing management prevents their expression. Hodgson (1982) suggests that under intensively grazed and relatively simple swards sheep would graze the surface horizons indiscriminately. However, Milne *et al* (1982) reported that the proportion of clover in extrusa samples from fistulated sheep grazing tall mixed grass/clover swards was higher than the proportion in the grazed horizons. Although differences in bite selection between cattle and sheep can be shown, they may be

too small to support theories of complementary use of vegetation, but they may explain the differences in the quality of the diet (Langlands and Sanson, 1976; Mulholland *et al*, 1977) selected by sheep and cattle.

Site selection

On a large scale, animals may concentrate their attention on particular sites within heterogeneous areas of vegetation (Hodgson, 1982). Heterogeneity caused by faeces deposition may be the most important single factor influencing site selection in intensively grazed swards. The subject has received considerable research attention in relation to the avoidance by cattle of areas contaminated with their faeces (Marsh and Campling, 1970; Brockington, 1972; Hodgson, 1974). Sheep are generally believed to be less sensitive to the presence of their own excreta (Arnold and Dudzinski, 1978), although rejection of areas contaminated by their own dung has been reported (Gibb *et al*, 1972; Hodgson and Forbes, 1980). Direct investigations on the reaction of sheep and cattle to the dung of their own compared with the reaction to the opposite species are few. Forbes (1982) showed that cattle were more sensitive to their own dung than to the sheep dung, whereas sheep were as sensitive to their own dung as to that of cattle. In a series of studies quoted by Nolan (1980), it was found that under combined grazing both species spent more time grazing the tall herbage associated with dung, and sheep spent twice the time spent by cattle, but in these studies the high vegetation was not identified as associated with cattle or sheep dung. The fact that cattle spent more time on the tall herbage at the end of the season (Nolan, 1980), suggests that grazing pressure may not have been maintained (Greenhalgh and

Reid, 1969). Although more information is necessary to make firm conclusions, it is reasonable to expect that under intensive grazing, the wastage of herbage around dung pats may be less under mixed stocking than under single stocking.

HERBAGE INTAKE

On intensively grazed swards herbage intake is likely to be limited by the effect of stocking rate, herbage quality and herbage mass (Hodgson, 1976). It is likely that increased growth rate, if not controlled by an increase in stocking rate, results in increased intake per animal, although sward condition (i.e. structure or sward surface height) may affect animal intake independently (Hodgson, 1977; Hodgson, 1982). The existing evidence suggests that the ingestive behaviour of cattle and sheep is similarly affected by variations in sward characteristics (Jamieson and Hodgson, 1979; Hodgson, 1981b). It is frequently suggested that under extreme conditions cattle have difficulties in harvesting due to anatomical limitations set by their bigger mouth parts (Leigh, 1974). However, grazing sheep seldom penetrate into the horizons containing pseudostem (Barthram, 1980) even at the expense of severe reduction in their herbage intake.

On the other hand, if anatomical characteristics give sheep advantages in harvesting forage at low herbage masses (Leigh, 1974; Van Dyne *et al*, 1980), complementarity can not be expected when both cattle and sheep are grazed together. In this case, advantages in total output can still result from mixed stock if the advantages of one species is not cancelled out by the disadvantage of the other.

CONCLUSIONS

There are managerial and financial consequences and epidemiological

reasons to justify advantages in running mixed stocking systems. However, there is not enough experimental evidence even from single species grazing to indicate whether rates of herbage growth and utilisation are likely to be greater in mix-stocked systems than in single species systems. Better understanding of the tissue fluxes and the implications to the stability of food supply even on single species grazing would be necessary before firm conclusions can be drawn. Swards grazed by sheep have higher tiller densities than swards grazed by cattle, although the mechanisms involved are not yet clear. This difference in tiller density might create differences in net herbage production, although phenotypic plasticity of individual tillers (i.e. modification of growth and senescence rates) may compensate for the numerical differences and net production of the population remained unchanged. However differences in tiller density may affect stability of the net herbage production rate, either in the short or the long term.

Differences in the botanical and morphological composition of the diet selected under intensive grazing, may not be large enough to support theories based on complementary use of the vegetation when both cattle and sheep are grazed together, but these differences might explain the variation in the quality of the diet selected. Grazing behaviour in general and particularly in the vicinity of the dung pats seems to be similar between species, but herbage wastage round dung pats might be expected to be lower in mixed grazing systems than under single-species grazing.

EXPERIMENTAL

CHAPTER 3

GREENHOUSE EXPERIMENTS

INTRODUCTION

Dry matter flux in grassland systems may be estimated by measurements of rates of tissue formation, tissue decay and tissue removal per population unit (e.g. tiller) combined with estimates of population densities (Bircham, 1981b; Hodgson *et al*, 1981; Davies, 1981). Changes in leaf length are the result of elongation and defoliation of new leaves and defoliation and senescence of existing leaves. On continuously stocked swards, some assumptions have to be made in order to estimate the elongation rate of the laminae defoliated between two observation periods. Two models have been used. Hodgson and Ollerenshaw (1969) obtained the estimation from the mean elongation rate for all undefoliated laminae of similar rank over the same interval of time. On the other hand, Bircham (1981b) used the rate of extension of the same leaf in the previous period of time. In using the first model, the assumption has to be made that defoliation intensity, tiller size and developmental stage have no effect on the rate of elongation of new leaves. The second model assumes that elongation rate is not affected either by defoliation, leaf age or weather conditions.

The two experiments described here were designed to examine the effect of controlled defoliation under sward-like conditions on tiller growth and development to augment existing information from spaced plants and from grazed swards. The principal interest was in leaf extension rates and tiller associations but the implications of alternative correction models were also investigated since these have not been examined quantitatively before.

Leaf elongation rate

The extension rate of emerged elongating leaves is highly

correlated with temperature and moisture deficit, and poorly correlated with light energy (Langer, 1954; Davidson and Milthorpe, 1966; Silsbury, 1970; Peacock, 1975a, b, c; Leafe *et al*, 1975; Thomas, 1977). Thus the daily environmental variation in temperature and water stress causes diurnal fluctuation in laminae elongation rates (Allison, 1963; Williams and Biddiscombe, 1965). Reductions in nitrogen supply have a direct effect on the rate of leaf elongation (Leafe *et al*, 1975), but leaf extension under controlled conditions is constant from leaf emergence to ligule appearance (Wardlaw, 1969; Robson, 1973; Torvell, unpublished). Thus if current elongation rate is estimated from the previous period it may be over- or under-estimated depending on the previous weather environment.

The rate of leaf extension may be inversely related to severity of defoliation (De Lucia Silva, 1974; Wade, 1979; Grant *et al*, 1981a). However, such response has not been found in spaced plants indoors, (Davidson and Milthorpe, 1966; De Lucia Silva, 1974) although Davidson and Milthorpe (1966) suggested that extreme defoliation (all young leaves removed) reduced elongation rates, and that level of mineral nutrients interacted with treatments on leaf extension rates following defoliation.

Tiller size

Tiller size seems to affect leaf elongation rates. Torvell (unpublished data) found that the leaf elongation rate of independent vegetative tillers (parents) was greater than that of their associated tillers (daughters). Although it has been shown in plants of *Lolium multiflorum* Lam. that defoliated tillers divert some assimilates from undefoliated tillers (Marshall and Sagar, 1965; Marshall and Sagar, 1968; Gifford and Marshall, 1973)

it is not clear if the supply of assimilates is enough to support the same rates of leaf extension of defoliated and undefoliated tillers. In ungrazed swards, tiller size distribution seems to be positively skewed and changes in population structure appear to be related to tiller density (Obeid, Machin and Harper, 1967; Naylor, 1976). Under grazing, additional changes in population structure might occur if defoliated tillers eventually become smaller than undefoliated tillers.

From the published information it seems unlikely that the assumptions made in using either model are strictly valid, since it is not clear if a single defoliation would affect the elongation of the currently expanding lamina.

MATERIALS AND METHODS

Two greenhouse experiments were designed to provide information on the effect of severity of defoliation and proportion of tillers defoliated upon the elongation rate of leaf lamina. The effect of size of the tiller and severity of the defoliation upon lamina elongation rate was also investigated.

EXPERIMENT 1

General

Pure swards of S23 *Lolium perenne* were sown on soil in four boxes (40 cm x 60 cm x 11 cm deep) in January 1980, and grown in a glass-house at a temperature above 10°C without artificial lighting. A compound starter fertiliser (S.A.I. No. 1 N:P:K = 15:15:21 units) supplying 6 g $m^{-2}N_2$ was applied at sowing and extra fertiliser (Nitram) at an equivalent rate of 9 g $m^{-2}N_2$ was applied on three occasions over the period between the end of February to middle of April. The boxes were watered regularly.

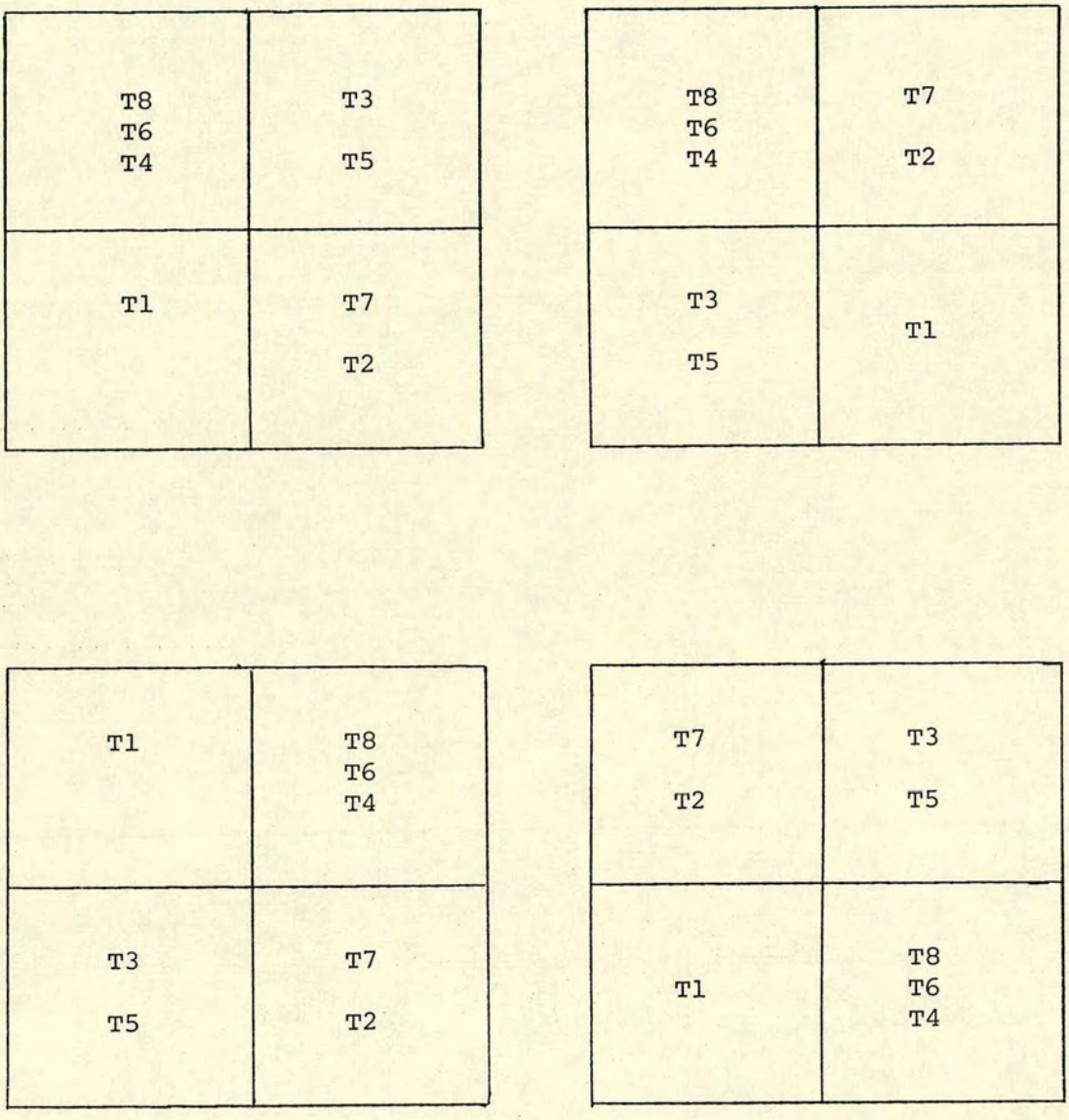


Figure E1.1. The experimental layout for Experiment 1; T1 to T8 treatments described in Table E1.1.

Table E1.1. Description of the treatments applied to tillers in microswards of S23 perennial ryegrass on the 4th May 1980.

Treatment	Treatment Description
T1 (50 A)	40-50% of each leaf lamina removed from all the tillers in a quarter of a box.
T2 (50 S)	40-50% of the lamina removed from 10 selected tillers; remaining tillers untouched (c.f. T1).
T3 (100 A)	100% of each leaf lamina removed from all the tillers in a quarter of a box.
T4 (100 S)	100% of lamina removed from 10 selected tillers; remaining tillers untouched (c.f. T3).
T5 (100 S + Sh)	100% of each leaf lamina removed + 2 mm sheath from 10 tillers in the same quarter as T3.
T6 (100 S + Sh)	100% of lamina removed + 2 mm sheath from 10 tillers in the same quarter as T4.
T7 (C)	Undefoliated control tillers in the same quarter as T2.
T8 (C)	Undefoliated control tillers in the same quarter as T4.

On May 4th, eight treatments were applied to each of ten individual tillers chosen at random from each quarter of each box. The treatments, which are shown in the Table E1.1 were the result of a basic combination of two levels of intensity of defoliation, lenient (40-50% of each leaf lamina removed) and severe (100% of each lamina removed) and two levels of modification on neighbouring tillers, total (all tillers in a quarter defoliated) and partial (only the ten random selected tillers defoliated). Four additional treatments (two extra in quarters with T4 and one extra in quarters with T2 and in quarters with T3) were applied to ten extra tillers randomly chosen in each quarter (Figure E1.1). Two controls, one in each level of intensity of defoliation, and two extra-severe defoliations (2 mm of the pseudostems removed as well as all leaf laminae) in the two levels of neighbouring modification. The treatments were allocated at random in four replications.

Measurement on individual tillers

Ten tillers per treatment within each quarter were selected at random and marked for detailed observation. The procedure adopted during the marking process was to place a "Weldmesh" 11 mm grid over a quarter of a box and points were chosen according to randomised "x" and "y" co-ordinates and tillers selected on a vertical first hit basis. If the co-ordinates of the point were in a 22 mm perimeter of the quarter the points were re-randomised to avoid possible edge effects. The selected tillers were identified with fine plastic-coated wire rings of a different colour for each treatment. The length of the lamina (i.e. from the ligule to tip or to the lower edge of the yellow-region) was recorded for each leaf

of each tiller, three days before and again immediately before the treatments were applied. Similar observations were made 3, 6 and 13 days after the treatments were applied.

EXPERIMENT 2

General

Pure swards of S23 perennial ryegrass were sown on soil in three boxes (43 x 35 x 15 cm deep) in October 1979 and placed in a heated greenhouse under supplementary light (150 Wm^{-2}) for 12 hours each day. A compound starter fertiliser (John Innes No. 2, N:P:K = 23:11:10) supplying 6 g $m^{-2}N_2$ was applied at sowing. The swards were cut five times, to an aftermath height of 3 cm, between November 1979 and January 1980, and a nitrogen fertiliser equivalent to 2 g $m^{-2}N_2$ was applied every second cut. Between January and February, the swards were cut four times to aftermath height of 1.5 cm to stimulate tillering and equivalent of 4 g $m^{-2}N_2$ was applied every second cut. From the beginning of March until the allocation of treatments, the swards were cut weekly to 2.5 cm and every second week 2 g $m^{-2}N_2$ was applied. The boxes were watered regularly. On the 15th of May, four treatments were applied to each of ten independent vegetative tillers and their associated dependent tillers (parent and daughter pairs), chosen at random from each quarter of a box (see procedure for Experiment 1) and those which had a visible attached tiller were marked. The bigger tiller of the pair was assumed to be the parent and the smaller to be the daughter. The treatments shown in Table E2.1 were the result of removing all combinations of 0% or 100% of every leaf lamina of parents and daughter tillers. The treatments were replicated in three similar boxes.

Table E2.1. Description of treatments applied to parent (P) and daughter (D) tillers in microswards of S23 perennial ryegrass on the 14th May 1980.

Treatment	Treatment Description
1 (only P)	100% of each lamina leaf of the parent tiller defoliated. Daughter untouched.
2 (only D)	100% of each lamina leaf of the daughter tiller defoliated. Parent untouched.
3 (P and D)	100% of each lamina of both parent and daughter tillers defoliated.
4 (C)	Both parent and daughter tiller undefoliated.

Measurements on individual tillers

Ten pairs of tillers within each quarter of a box selected as described above were used for detailed observations. The units (parent and daughter) were identified with rings of plastic coated wire of different colours for each treatment. The length of each green leaf lamina from the ligule to the tip, or to the lower edge of the yellow region, was recorded in each tiller, six and thirteen days after defoliation. At the end of the experimental period all tillers were cut at ground level, dried at 80^{o}C for eight hours, and weighed.

Statistical analysis

The pooled standard error of the mean ($SE\bar{x}$) for comparison of the mean treatment effects was calculated by analyses of variance. The data in Experiment 1 were classified in time, treatment, replication and sub-replicates (tillers) and in Experiment 2 in parent and daughter classes also.

In Experiment 1 there were eight treatments allocated to four

Table E1.2. Analysis of variance for Experiment 1

Source of variation	D.F.
Replicates	3
SUBA	3
Residual A	9
Total	12
Rep. Quart. Tiller	144
Period	3
Period.SUBA	9
Residual	468
Total	480
SUBA.SUBB	4
PERIOD.SUBA.SUBB	12
Residual A.B.	624
Total	640
Grand total	1279

quarters of a box. The treatment effect was unbalanced and in this kind of design the degrees of freedom represented by the main effect of the basic factorial (T1, T2, T3 and T4) and the extra treatments (T5, T6, T7 and T8) are all estimated with less efficiency within quarters than is their interaction (Cochran and Cox, 1956). This was overcome by using pseudo factors to partition treatments into two pseudo terms, each of which was balanced. Three degrees of freedom for treatments were confounded with quarters in each replicate, and the degrees of freedom for treatments were determined by regarding treatments as if they were represented by two sub-factors (SUBA and SUBB; Table E1.2). The treatment effect is equivalent to the interaction of the two sub-factors (SUBA.SUBB in Table E1.2) and the standard error of the differences between means was calculated from equation 1:

$$SED = \frac{12\sigma w^2 + 11\sigma b^2}{n}; \quad \text{i.e.} \quad \frac{12x(\text{Residual A}) + 11x(\text{Residual A.B})*}{460} \qquad \text{e.q. 1}$$

*See Table E1.2

RESULTS

General

Lamina elongation rate was calculated i, as daily increment in green lamina length of the leaf currently in expansion when the experiment started and ii, as daily increment in green lamina length of all leaves both currently expanding and new which appeared during the experiment. The first calculated elongation rate is of obvious interest in the discussion of the assumptions made to estimate growth between two periods of observation under continuous stocking,

Table E1.3. Lamina leaf elongation rate (mm tiller^{-1} day^{-1}) of tillers in main treatments combinations 0-3, 3-6 and 6-13 days after defoliation. (Only leaves currently in expansion when treatments started are included).

Defoliation treatment†	0-3 days	3-6 days	6-13 days
Severe (T3+T4)	4.7	1.3	0.2
Lenient (T1+T2)	4.6	1.1	0.5
Sample tillers (T2+T4)	5.4	1.4	0.4
All tillers (T1+T3)	3.9	1.1	0.3
Severe + sheath (T5+T6)	3.9	1.3	0.3
Control (T7+T8)	3.5	0.7	0.3
$SE_{\bar{x}}$	0.33	0.075	0.082

†Comparisons in this and later tables between complementary pairs of treatments (e.g. (T3+T4) and (T1+T2) and between these pairs and controls (T7+T8) on treatments involving partial defoliation of sheaths (T5+T6).

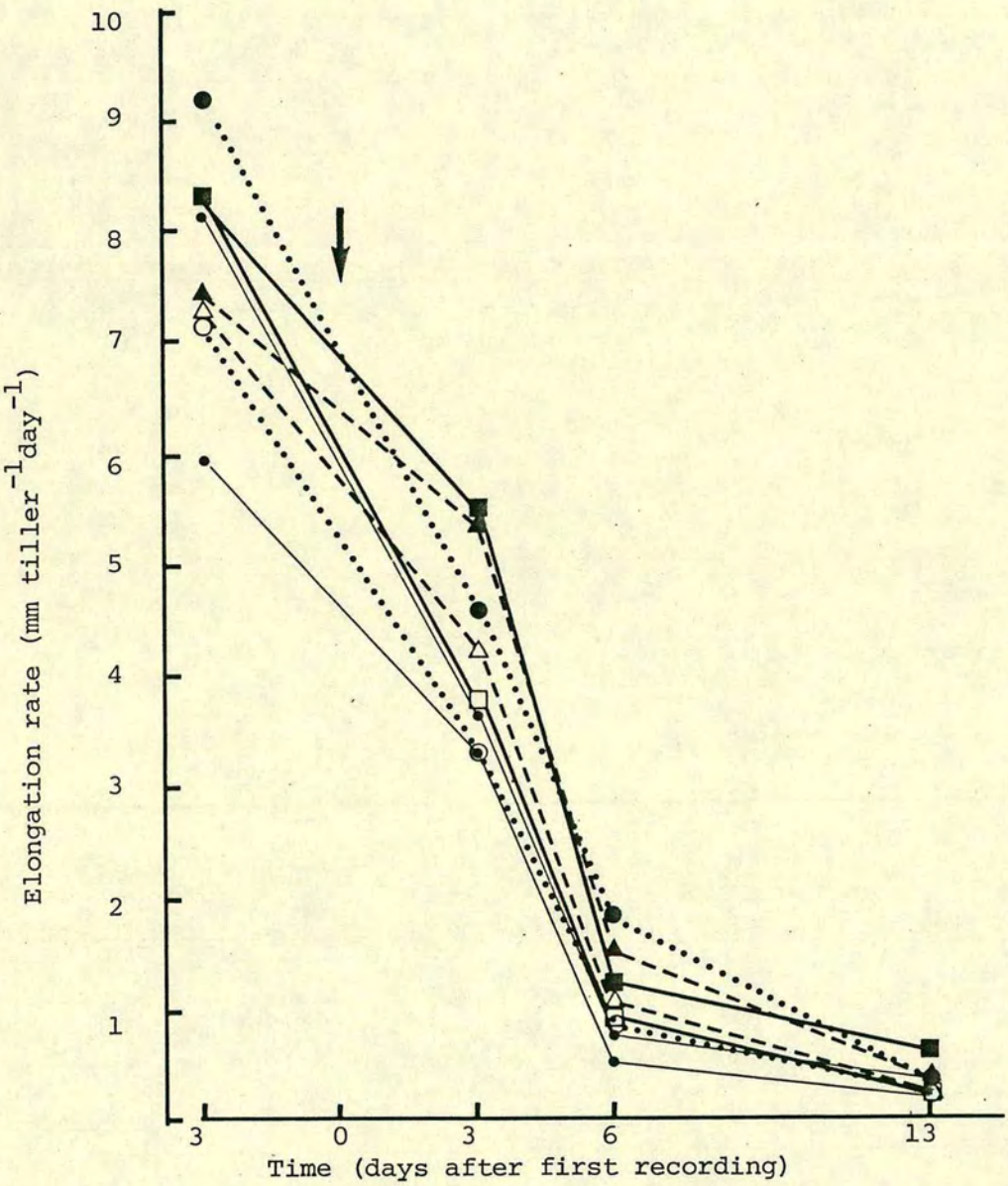


Figure E1.2. Leaf lamina elongation rate (mm tiller^{-1}day^{-1}) of individual ryegrass tillers during 0-3 days before and 0-3, 3-6 and 6-13 days after defoliation (⬇) (only leaf in expansion at the moment of starting the experiment) □ T1(50A), ■ T2(50S), △ T3(100A) ▲ T4(100S), ○ T5(100S+Sh), ● T6(100S+Sh), • T7 and T8 (C).

when defoliation has taken place. The second calculated elongation rate provides an estimate of the effect of treatment on total leaf production and it may also be relevant to check extra variation due to other uncontrolled causes such as water or nutrient deficits. In addition, senescence and net elongation rates calculated from the total number of leaves of each tiller are presented.

EXPERIMENT 1

Elongation rate of the leaves currently expanding at the time of defoliation

The elongation rate (mm tiller^{-1}day^{-1}) of the leaf lamina in expansion at the moment when the measurement started, calculated over periods of 0-3 days before and 0-3, 3-6 and 6-13 days after defoliation is depicted in Figure E1.2. Overall elongation rate declined as leaf age increased, from 7.7 mm tiller^{-1}day^{-1} for 0-3 days before defoliation, to 4.2, 1.1 and 0.3 ± 0.14 mm tiller^{-1} day^{-1} for 0-3, 3-6 and 6-13 days after defoliation respectively (Figure E1.2). In one of the controls (T7) elongation rate was lower than in all other treatments 0-3 days before defoliation. The interaction time x treatment was significant ($P< 0.05$) and this interaction was still significant ($P< 0.05$) when 0-3 days before defoliation was excluded from the analysis.

On the basic factorial (T1, T2, T3 and T4) the interaction severity of defoliation x defoliation of the neighbouring tillers was not significant. Defoliation of the neighbouring tillers reduced the rate of elongation during the first 0-3 and 3-6 days after defoliation (Table E1.3). When all tillers were defoliated elongation rate was lower than when only 10 tillers per treatment were defoliated,

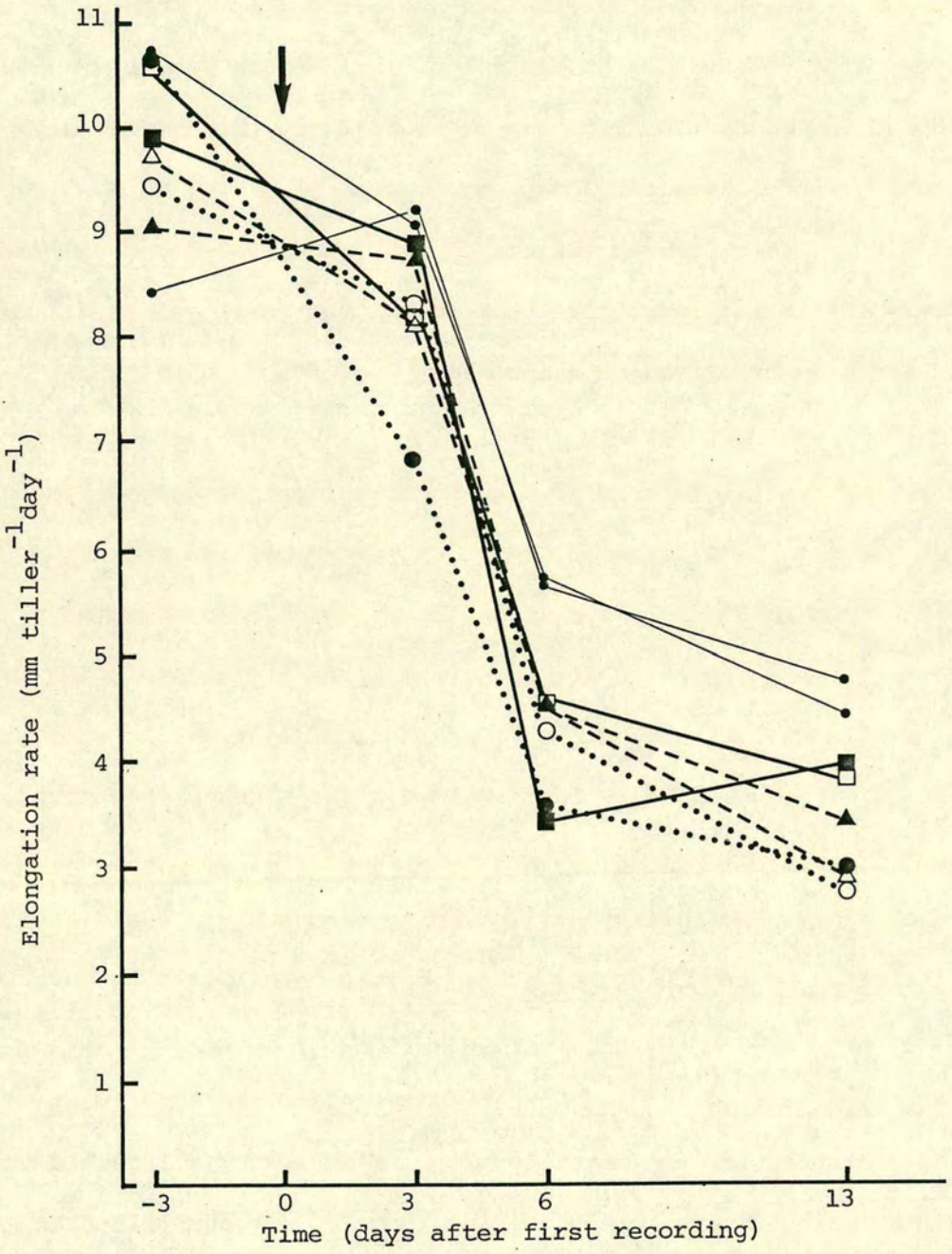


Figure E1.3. Leaf laminae elongation rate (mm tiller^{-1}day^{-1}) of individual ryegrass tillers during 0-3 days before and 0-3, 3-6 and 6-13 days after defoliation (↓). (All leaves included). □ T1(50A), ■ T2(50S), △ T3(100A), ▲ T4(100S), ○ T5(100S+Sh), ● T6(100S+Sh), • T7 and T8 (C).

independent of the severity of defoliation (T1 + T3 vs T2 + T4; 3.9 vs 5.4 ± 0.33 and 1.1 vs 1.4 ± 0.07 mm tiller^{-1}day^{-1}, $P < 0.05$ 0-3 and 3-6 days after defoliation respectively). When severity of defoliation was 100% of every leaf lamina plus 2 mm of sheath (T5 and T6) elongation rate was lower in those tillers on which the neighbouring tillers were completely defoliated (3.3 vs 4.5 ± 0.66 and 0.8 vs 1.8 ± 0.15 mm tiller^{-1}day^{-1}, $P < 0.05$ 0-3 and 3-6 days after defoliation respectively) although the first comparison was not significant at the 0.05 level.

The elongation rate of undefoliated control tillers immediately after the treatments were applied was not significantly different from the rate of elongation of tillers where all the neighbours were defoliated (T1 and T3), but it was lower than the elongation rate of the tillers where the neighbours were not defoliated (T2 and T4) (Table E1.3). Three to 6 days after defoliation the elongation rate of the controls was lower than on all the other treatments, but all the differences disappeared 6-13 days after defoliation. The analyses were repeated using laminae length before and after defoliation or leaf elongation rate before defoliation as covariates, but no covariate effects were significant.

Elongation rate of all leaves appearing during the experiment

Elongation rates (mm tiller^{-1}day^{-1}) including all the leaves that appeared during the experimental period are summarised in Figure E1.3. The elongation rate 0-3 days before defoliation was not different from the rate of elongation 0-3 days after defoliation (9.7 vs 8.5 ± 0.22 mm tiller^{-1}day^{-1}) but after defoliation the elongation rate declined over time (8.4 vs 4.5 vs 3.6 ± 0.22 mm tiller^{-1} day^{-1}, $P < 0.05$; Figure E1.3; Table A1.2, Appendix A1).

Table E1.7. Net laminae elongation rate (mm tiller^{-1}day^{-1}) of individual ryegrass tillers 0-3 days before and 0-3, 3-6 and 6-13 days after defoliation.

Treatment	0-3 days before	0-3 days after	3-6 days after	6-13 days after
1 (50A)	9.7	5.7	3.2	2.5
2 (50S)	9.2	6.6	2.1	3.0
3 (100A)	8.9	7.8	3.4	2.1
4 (100S)	8.2	8.7	4.3	2.7
5 (100S+Sh)	9.6	6.9	4.5	2.9
6 (100S+Sh)	8.8	8.3	4.5	3.4
7 (C)	7.6	7.6	2.9	2.6
8 (C)	9.8	6.2	2.4	2.5
$SE_{\bar{x}}$	0.68	0.88	0.62	0.33

Table E1.6. Leaf lamina senescence rate (mm $tiller^{-1}day^{-1}$) of individual ryegrass tillers 0-3 days before and 0-3, 3-6 and 6-13 days after defoliation.

Treatment	0-3 days before	0-3 days after	3-6 days after	6-13 days after
T1 (50A)	0.4	2.5	1.3	0.4
T2 (50S)	0.5	2.1	1.5	0.3
T3 (100A)	0.8	0.0	0.0	0.0
T4 (100S)	0.7	0.0	0.0	0.0
T5 (100S+Sh)	0.9	0.0	0.0	0.0
T6 (100S+Sh)	0.7	0.0	0.0	0.0
T7 (C)	0.8	1.5	2.7	0.4
T8 (C)	0.9	2.8	3.3	0.4
$SE\bar{x}$	0.37	0.31	0.43	0.22

Table E1.5. Leaf appearance rate (leaves tiller^{-1}day^{-1} and leaf appearance intervals (days) of tillers in main treatments combinations over the period 5 to 22 of May 1980.

Defoliation treatment†	Leaf appearance rate (leaves tiller^{-1} day^{-1})	Leaf appearance interval (days)
Severe (T/+T4)	0.07	15.4
Lenient (T1+T2)	0.07	14.1
Sample tillers (T2+T4)	0.07	15.4
All tillers (T1+T3)	0.07	14.3
Severe + Sheath (T5+T6)	0.06	15.6
Control (T7+T8)	0.08	12.2
$SE_{\bar{x}}$	0.004	1.26

$SE_{\bar{x}}$ calculated as the $SE_{\bar{x}}$ of the increase of leaf appearance rate

†for treatment comparisons see footnote to Table E1.3.

Table E1.4. Leaf lamina elongation rate (mm $tiller^{-1}day^{-1}$) of tillers in main treatments combinations 0-3, 3-6, and 6-13 days after defoliation (all levels included).

Defoliation treatment†	0-3 days	3-6 days	6-13 days
Severe (T3+T4)	8.4	4.5	3.2
Lenient (T1+T2)	8.5	4.0	3.8
Sample tillers (T2+T4)	8.7	4.0	3.6
All tillers (T1+T3)	8.2	4.5	3.3
Severe + complete + sheath (T5+T6)	7.6	3.9	2.9
Control (T7+T8)	9.0	5.6	4.5
$SE_{\bar{x}}$	0.57	0.31	0.22

†for treatment comparisons see footnote to Table E1.3.

The interaction treatment x time was significant ($P < 0.05$) even when elongation rate before defoliation was excluded from the analysis. Immediately after defoliation there were no significant differences in leaf elongation rate among treatments although, overall, the elongation rate of the controls was higher than the elongation rate of the defoliated tillers (Table E1.4).

The rate of leaf appearance for all the main treatments (leaves appeared tiller^{-1}day^{-1}) is given in Table E1.5. Defoliation overall reduced the rate of leaf appearance (0.07 vs 0.08 ± 0.004 leaves tillers^{-1}day^{-1}) but among defoliation treatments there was not a clear pattern.

Leaf lamina senescence rate

The rates of lamina senescence (mm tiller^{-1}day^{-1}) for all the treatments is given in Table E1.6. The rate of senescence was similar in all treatments before defoliation and the interaction time x treatment was significant even when 0-3 days before defoliation was excluded from the analysis. In the controls (T7 and T8) and in the leniently defoliated treatments (T1 and T2) the rate of leaf lamina senescence was lower before defoliation than 0-3, and 3-6 days after defoliation, but was not different from 6-13 days after defoliation. In the treatments severely defoliated (T3 and T4) and in those with 2 extra mm of sheath removed (T5 and T6) the rate of leaf senescence was zero even 13 days after defoliation.

Net elongation rate

The net elongation rate including all the leaves that appeared during the experimental period for all the treatments is given in Table E1.7. Net elongation rate before defoliation was higher than the net rate of elongation 0-3 days afterward (9.0 vs 7.2 ± 0.29 mm

Table E2.2. Lamina elongation rate (mm tiller^{-1}day^{-1}) of ryegrass vegetative independent tillers (P) and of their associated tiller (D) during 0-6 and 6-13 days after defoliation. (Only leaves currently expanding at the time of defoliation).

Treatment	0-6 days		6-13 days	
	P	D	P	D
1 (only P)	5.9	4.7	2.0	1.2
2 (only D)	6.5	4.8	1.4	0.8
3 (P and D)	6.6	4.7	1.7	1.2
4 (C)	5.6	4.8	1.2	1.5
$\bar{x}$	6.1	4.8	1.6	1.2
SE$\bar{x}$	0.54		0.33	

Table E2.3. Lamina leaf elongation rate (mm tiller^{-1}day^{-1}) of ryegrass vegetative independent tillers (P) and their associated tiller (D) during 0-6 and 6-13 days after defoliation (total existing at defoliation plus new leaves).

Treatment	0-6 days		6-13 days	
	P	D	P	D
1 (only P)	7.7	6.9	5.1	5.5
2 (only D)	8.6	6.4	7.5	2.9
3 (P and D)	7.7	5.6	4.9	2.6
4 (C)	8.7	5.8	7.3	4.7
$\bar{x}$	8.2	6.1	6.2	3.9
SE$\bar{x}$				0.38

tiller^{-1}day^{-1}, $P < 0.05$).

The interaction treatment x time was significant ($P < 0.05$) but it disappeared when elongation rate before defoliation was excluded from the analysis. Immediately after defoliation there were no significant differences in net elongation rate between individual treatments. The net elongation rate was higher on average in the severe than in the leniently defoliated tillers in 0-3 days after defoliation (8.2 vs 6.2 ± 0.623 mm tiller^{-1}day^{-1}, $P < 0.05$) but the difference disappeared 6-13 days after defoliation.

EXPERIMENT 2

The lamina elongation rate is presented as in Experiment 1, and senescence and net elongation rates including all the leaves are presented too.

Elongation rate

Table E2.2 gives the elongation rate (mm tiller^{-1}day^{-1}) of the lamina currently in expansion at the time when the treatments were applied. The rate was calculated on parent and daughter tillers over periods of 0-6 and 6-13 days after defoliation. Overall elongation rate declined on both parent and daughter tillers as leaf age increased, from 6.1 to 1.6 and 4.8 to 1.2 mm tiller^{-1}day^{-1}, on parents and daughter tillers respectively. Defoliation treatments did not affect elongation rate either on parent or daughter tillers. However, parent laminae elongated at a higher rate than the laminae on daughter tillers (6.1 vs 4.8 ± 0.539 and 1.6 vs 1.2 ± 0.326 mm tiller^{-1}day^{-1}, $P < 0.05$ for 0-6 and 6-13 days after defoliation respectively).

Elongation rate including all leaves appeared during the experimental period

The elongation rates (mm tiller^{-1}day^{-1}) including all the leaves

Table E2.4. Leaf appearance rate (leaves $tiller^{-1}day^{-1}$) and leaf appearance intervals (days) of parent and daughter tillers over the period 15 to 28 May 1980.

	Leaf appearance rate (leaves $tiller^{-1}day^{-1}$)		Leaf appearance interval (days)	
Treatment	Parent	Daughter	Parent	Daughter
1 (only P)	0.07	0.07	13.5	13.5
2 (only D)	0.09	0.06	11.5	17.9
3 (P and D)	0.07	0.05	15.0	21.7
4 (C)	0.09	0.07	11.1	14.5
$\bar{x}$	0.08	0.06	12.8	16.9
$SE\bar{x}$		0.007		1.31

Table E2.5. Senescence rate (mm $tiller^{-1}day^{-1}$) of ryegrass vegetative independent tillers (P) and of their associated tiller (D) during 0-6 and 6-13 days after defoliation.

Treatment	0-6 days		6-13 days	
	P	D	P	D
1 (only P)	0.0	1.2	0.0	2.0
2 (only D)	2.1	0.0	2.2	0.0
3 (P and D)	0.0	0.0	0.0	0.0
4 (C)	1.8	2.7	3.4	2.6
$\bar{x}$	1.0	1.0	1.4	1.1
$SE\bar{x}$	0.26			

that appeared during the experimental period for both parent and daughter tillers are given in Table E2.3 .

The rate of leaf extension was higher on parent tillers than on daughter tillers and higher 0-6 days than 6-13 days after defoliation (8.2 vs 6.1 and 6.2 vs 3.9 ± 0.38 mm $tiller^{-1}day^{-1}$, $P < 0.05$). The interaction time x tiller generation was not significant but the interactions tiller generation x defoliation treatment and time x tiller generation x defoliation treatment were ($P < 0.05$). When parent tillers were defoliated, the difference in elongation rate after defoliation between parent and daughter was not significant. However, when daughter tillers were defoliated, their elongation rate was lower than their parent's elongation rate (T2 and T3) but, when parents were not defoliated, the elongation rate of the daughters was further depressed than when both parent and daughter tillers were defoliated. When the analyses were repeated using laminae length before defoliation as a covariate, neither tiller generation nor defoliation x time effects were significant.

The rate of leaf appearance for parents and daughter tillers in the different defoliation treatments are given in Table E2.4. Leaf appearance rate was higher on parent than on daughter tillers (0.08 vs 0.06 ± 0.003 leaves, $tiller^{-1}day^{-1}$, $P < 0.05$) and it was reduced by defoliation (0.08 vs 0.06 ± 0.005 leaves, $tiller^{-1}day^{-1}$, $P < 0.05$).

Senescence rate

The rate of leaf senescence (mm $tiller^{-1}day^{-1}$) for both parent and daughter tillers is given in Table E2.5 . The overall rate of leaf senescence was lower 0-6 than 6-13 days after defoliation,

Table E2.6. Lamina net elongation rate (mm tiller^{-1}day^{-1}) of ryegrass vegetative independent tillers (P) and of their associated tiller (D) during 0-6 and 6-13 days after defoliation.

Treatment	0-6 days		6-13 days	
	P	D	P	D
1 (only P)	7.7	5.7	5.1	3.5
2 (only D)	6.4	6.4	5.4	2.9
3 (P and D)	7.7	5.6	4.9	2.6
4 (C)	6.8	3.1	3.8	2.2
$\bar{x}$	7.2	4.4	4.8	2.8
$SE\bar{x}$	0.46			

and it was not affected by tiller generation (1.0 vs 1.0 and 1.4 vs 1.1 ± 0.26 mm $tiller^{-1}day^{-1}$, $P < 0.05$).

Tillers from which 100% of every leaf was removed did not show any signs of senescence during 13 days after defoliation.

Net elongation rate

The net rate of leaf elongation (elongation minus senescence; mm $tiller^{-1}day^{-1}$) for both parent and daughter tillers is given in Table E2.6 and followed a similar pattern to leaf extension rate. Both parent and daughter tillers rate of net change were higher 0-6 than 6-13 days after defoliation (7.2 vs 4.8 and 4.4 vs 2.8 ± 0.46 mm $tiller^{-1}day^{-1}$, $P < 0.05$). The net lamina elongation rate was lower in daughter tillers than in parent tillers but when parent tillers were undefoliated, net changes in parent and daughter tillers were initially similar. However, 13 days after defoliation the rate of net change in daughter tillers was further depressed than that of the parent tillers. On the other hand, net accumulation rate in the defoliated parent was higher than in the undefoliated parent 6 days after defoliation (7.7 vs 6.6 ± 0.32 mm $tiller^{-1}day^{-1}$, $P < 0.05$) but the differences disappeared by the end of the experiment.

Tiller weight

The weight of both parent and daughter tillers for all the treatments (mg $tiller^{-1}$) at the end of the experimental period are given in Table E2.7. Overall, parent tillers were significantly heavier ($P < 0.05$) than daughter tillers.

Table E2.7. Weight (mg tiller^{-1}) of independent ryegrass vegetative tillers (parents) and of their associated tillers (daughters) harvested from microswards under different defoliation treatments.

Treatment	Parent	Daughter
1 (only P)	18.4	15.0
2 (only D)	29.4	7.9
3 (P and D)	16.6	7.6
4 (C)	32.9	14.5
SED	1.62	

DISCUSSION

General

The elongation rate of the leaves in visible extension when the experiment started declined as the experiment proceeded (Figure E1.2 and Table E2.2) and so did the elongation rate per tiller (i.e. considering all extending leaves) in both experiments (Figure E1.3 and Table E2.3). Under controlled conditions leaf extension rate from a particular leaf appears to be constant from lamina emergence to ligule appearance, and then declines abruptly to zero, either in single plants (Wardlaw, 1969; L. Torvell, personal communication) or in microswards (Robson, 1973). Because a new leaf appears before the preceding leaf is fully expanded the rate of elongation per tiller under controlled conditions appears to be constant as well, either in spaced plants (Mitchell, 1955) or in microswards (Robson, 1973). The declining elongation rate of the leaves in expansion at the beginning of the experiment was presumably

the result of a population of leaves with different age classes being used. When populations of unsynchronised leaves have been observed, the accumulated extension after defoliation has been found to increase at a declining rate (Davidson and Milthorpe, 1966; De Lucia Silva, 1974). So the apparent decreasing rate of leaf elongation with time in these experiments could be regarded as the effect of leaves of different age progressively stopping growth, rather than as a decreasing rate of elongation with age in individual leaves. The decreasing elongation rate per tiller however, is difficult to explain since, in theory, a new leaf should have appeared before the elongation rate in the preceding leaf declined. This suggests that environmental factors may have been involved.

A sudden reduction in the rate of leaf elongation between 3 to 6 days after defoliation, followed by a slow reduction as the experiment proceeded, was observed. Similar rapid changes in elongation rate due to changes in temperature have been described in field experiments (Peacock, 1975a, b; Peacock, 1976). Mean daily temperature in the greenhouse ranged from 13.2^{o}C at the beginning to 16.7^{o}C at the end of the experiment, reaching 18.5 and 19.2^{o}C during the period 3 to 6 days after defoliation. The rate of leaf extension is very sensitive to plant stress and it has been used in studies of water and nitrogen deficit on plant physiology (Wardlaw, 1969; Boyer, 1970; Ryle, 1970). The boxes were watered daily, but as this was done manually some irregularity may be expected. However, even assuming that watering was not always done properly, any effect on the leaf elongation rate should have been random and short-lived since the elongation rate after rewatering is normally

resumed at similar levels as before the stress (Wardlaw, 1969). The boxes received nitrogenous fertiliser at a rate equivalent to 1 g m^{-2} day^{-1} N over the course of the experiment, a similar amount to that used in the field studies. However, the nitrogen applied was a soluble form and some degree of nitrogen shortage might have occurred.

Because of the uncertainty over the causes of the decline in elongation rate with time it is difficult to discuss any possible interaction between treatment and uncontrolled effects, and so some caution is necessary in the interpretation of these results.

Effect of a single defoliation on the subsequent lamina elongation rate of existing expanding leaves

Severity of defoliation did not affect the rate of leaf extension (Table E1.3 and E2.2). This result suggests that the leaf elongation after defoliation occurred from the portion still enclosed in the sheath tube (Begg and Wright, 1962; Davidson and Milthorpe, 1966) and carbohydrates used in this development may have come from the base of the lamina or from other tillers in the plant (Marshall and Sagar, 1965). The observation that expanding leaves have higher concentrations of soluble carbohydrates than expanded leaves and the apparent increase in concentration towards the base of the leaf (Davidson and Milthorpe, 1966) may give some support to the first alternative . However, the higher elongation rates on the treatments in which the neighbouring tillers were not defoliated (Table E1.3) suggests that some of the carbohydrates may have been drawn from other tillers in the plant. Elongation rate was not affected by the severest defoliation (2 mm sheath removed) and this may be expected since the zone of likely carbohydrate accumulation

was not affected. This result suggests that the rate of elongation of the leaf actively in expansion at the moment of cutting is not affected by a single defoliation. In other words the actively growing leaf appeared to reach the total length determined by the length of the sheath tube (Davies, 1977) independently of whether or not it had been defoliated.

Elongation rate seemed to be affected by tiller size, since it was higher in parent than in daughter tillers (Table E2.2) and this result confirms similar observations by L. Torvell (personal communication). Both results, the higher rate of elongation in parent than in daughter tillers and the negligible effect of a single defoliation on the subsequent leaf elongation rate, are relevant in the discussion of the estimate of the elongation rate of a leaf defoliated between two observation periods (see page 59).

The effect of defoliation on tiller growth rate

Leaf appearance interval

The leaf appearance interval was longer than those described for microswards in constant conditions (see Tables E1.5 and E2.4 and Robson, 1973) presumably due to the declining extension rate. The leaf appearance interval tended to be shorter in the tillers with higher rate of leaf elongation, i.e. the rate of leaf appearance (i.e. the inverse of the leaf appearance interval) tended to be lower in defoliated than in undefoliated tillers (see Tables E1.5 and E2.4). Davies (1974) and De Lucia Silva (1974) found that the initial effect of cutting in single plants was to reduce the rate of leaf appearance. Although in the current experiments the swards were under cutting for three months before the experiment started,

the severe defoliation applied may be comparable to less severe initial defoliation in spaced plants. However, if successive defoliations have the same effect on leaf appearance as in the present experiments, the growth rate of the swards severely and frequently defoliated may progressively decline in the long term. But frequent and severe cutting does not necessarily depress leaf appearance rate in the long term since adaptive changes occur, e.g. sheath length and lamina length become shorter under frequent defoliation (Jackson, 1976), and the rate of leaf appearance is adapted to the new equilibrium. Even faster rates of leaf appearance have been observed in swards frequently defoliated by sheep than on lax defoliation regimes (Grant *et al*, 1981a). The lower leaf appearance rate in the daughter compared with the parent tillers (Table E2.4) must have been the consequence of a slower rate of leaf elongation in the daughter tillers.

Leaf elongation rate per tiller

Three days after defoliation the elongation rate was not different in the controls and in the treated tillers (Table E1.4). Davidson and Milthorpe, (1966) reported that defoliation of expanded leaves in spaced plants did not affect the rate of leaf extension, but that the extension rate was reduced by removing the exposed laminae of expanding leaves or by removing all the leaves. On the other hand, De Lucia Silva (1974) found that defoliation of the oldest leaf in spaced plants depressed the subsequent rate of leaf elongation, while defoliation of the younger leaves had comparatively little effect. In the present experiments 100% or 50% of every visible lamina was removed, but under microsward condition the effects of

defoliation may have been offset by the movement of assimilates between neighbouring tillers. In Experiment 1 there was no association between lamina length either before or after defoliation and the subsequent elongation rate. However in Experiment 2, where the leaf length of the parent before defoliation was greater than that of the daughter, the differences in elongation rate between parent and daughter disappeared when leaf length before defoliation was used as covariate. In Experiment 1 the tillers were not selected by differences in size (i.e. parent and daughter) so the size structure of the tiller sample may have been different from that in Experiment 2.

De Lucia Silva (1974) found low linear correlations between lamina length before defoliation and subsequent elongation rate. However, S.A. Grant (personal communication) found quadratic correlations of 0.9 between the same variables. This may suggest that leaf length and elongation rate are related in a non-linear fashion. Thus tillers in De Lucia Silva's (1974) experiment and in Experiment 1 may have had longer laminae than those in Experiment 2, so the first tillers were in the flat part of the curve, while the tillers from the other experiment were in the linear phase. The rate of leaf extension per tiller may be inversely related to severity of defoliation (De Lucia Silva, 1974; Wade, 1979; Grant *et al*, 1981a) however, such a response has not been found in spaced plants indoors. Wade (1979) suggested that among other environmental factors the partial removal of the sheath tube under grazing may be in part responsible for these contradictory results. However, under grazing by sheep sheath removal does not appear to be great

(Barthram, 1980). In Experiment 1, the treatments in which 2 mm of sheath removed were intended to simulate grazing effects. The results would indicate that small portions of sheath removed during grazing are unlikely to affect leaf extension per tiller.

Lamina senescence rate

The absence of senescence in the severely defoliated tillers was a consequence of removal of virtually all mature tissue. In the leniently defoliated tillers the rate of leaf senescence was not different from the undefoliated tillers, though some reduction in senescence rate was expected since the oldest part of the leaves was removed. Tiller generation did not affect the rate at which leaves senesced. As parent tillers have bigger leaves a higher rate was expected. However, leaves in parent tillers were possibly intercepting more light than the leaves of the smaller tillers. Favourably illuminated leaves in the parent tillers may have senesced at a smaller relative rate and the rate per tiller may consequently have not been affected (Brougham, 1958; Hopkinson, 1966; Leopold, 1980).

Net elongation rate

Changes in weight per unit length or in specific leaf weight may occur throughout the life of a leaf (Vine, 1977; Robson and Deacon, 1978) and defoliation treatments may affect both variables (Grant *et al*, 1981$_a$). Thus, estimates of net leaf elongation rate may not accurately reflect differences in net changes in leaf weight per tiller. However in view of the limited treatment effects in these studies it is unlikely that there would be any serious disparity between conclusions based on net length and net weight changes.

The net rate of lamina elongation followed a similar pattern to total elongation rate in both experiments. However, the advantage in net elongation rate of the severely defoliated tillers was almost significant, 0-3 and 3-6 days after defoliation in Experiment 1 and 0-6 days after defoliation in Experiment 2. Similar balances between growth and senescence in individual tillers in spaced plants or swards when defoliated at different severities have already been reported (De Lucia Silva, 1974; Wade, 1979; Grant *et al*, 1981a).

The compensation between senescence and elongation rate appeared to be more evident in parent than in daughter tillers (Table E2.6). This result suggests that the balance between the two rates on a unit ground-area basis may depend on the relative proportion of parent and daughter tillers. Thus, in actively tillering swards at the beginning of the season (Langer *et al*, 1964), the balance between high growth rate and high senescence rate may not be as close as in autumn when tiller appearance rates slow down.

Effect of defoliation on distribution of tiller size

The net rate of leaf elongation was higher in parent than in daughter tillers and this suggests that small tillers have a high chance of remaining small, independent of the defoliation treatment. In undisturbed crops the size distribution of the populations appears to be positively skewed (Obeid, Machin and Harper, 1967; Naylor, 1976) and this may be largely explained by the fact of net growth rate of the big tillers being higher than that of the small tillers. Under grazing conditions bigger tillers have a higher chance of being defoliated (Hodgson and Ollerenshaw, 1969; McIvor and Watkin, 1973) and this would imply a normalisation of the size distribution in the

tiller population. However, as the defoliated parents still had higher net rates of leaf elongation than the undefoliated daughter tillers, the normalisation of the distribution of the population size may depend on the actual reduction of size in the bigger tillers.

The estimate of elongation when a leaf has been defoliated between two periods of observation

Grazing is characterised by the cyclic interactions between the grazing animal and its food. The study of fluxes of plant tissue and tillers allows the simultaneous assessment of the various process(es) taking place under grazing at any one time but, under continuous stocking, the assessment of some of the rates (growth and harvest rates in particular) is difficult since plant tissue may be defoliated between two observations. Thus if part of the growing tissue disappeared to animal consumption, the amount consumed has to be estimated indirectly.

Alternatively, the time between two observations may be reduced to minimise the risk of defoliation. However, there is a practical minimum limit to the length of time between two observations and, to be realistic, defoliation is always likely to occur between observations in a proportion of cases. Periods of 3-4 days seem to be adequate for this kind of study (Hodgson and Ollerenshaw, 1969; Bircham, 1981). Disappearance of growing tissue and cessation of growth may occur at any time during this period and this may introduce bias to the estimates. Estimating elongation of a leaf defoliated between two observations from the elongation rate in the previous measurement period (Model 1) (Bircham, 1981b) in theory may introduce three kinds of error. First,

a zero value may be ascribed because the lamina has been defoliated between observations in two or more consecutive periods; this is simply a practical limitation of computation. Second, an artificially high or low rate may be ascribed depending on changes in weather conditions over successive intervals (Williams and Biddiscombe, 1965; Peacock, 1975a, b, c). The third effect is the risk of overestimating elongation if a defoliated leaf completes expansion during the period for which correction is made. Some of these effects may be partially overcome by using a correction factor per tiller instead of per leaf, but the weather effect may still persist, and the risk of a zero value being ascribed is reduced but not eliminated. Alternatively the elongation rate of undefoliated expanding leaves on other tillers during the same period may be used in the estimate (Model 2) (Hodgson and Ollerenshaw, 1969). As a single defoliation does not appear to affect the subsequent elongation rate and the weather conditions are the same for all tillers, the above sources of bias are removed. However, the risk of overestimation if the leaf has completed elongation in the same period is not eliminated and two other problems arise by using this model. First, the average elongation rate of a population of leaves does not adequately reflect differences in tiller size (see Table E2.2) and, second, its use may reduce the variance of the estimate of mean extension rate. The first problem may be overcome by calculating different estimations for big and small tillers or for parent and daughter tillers, but the effect on the variance may have no solution.

There are no obvious reasons for choosing one model rather than the other, since there is not enough information to determine the size

and magnitude of the bias introduced by using a particular model, or the effect on the variance by using Model 2. Using published information from Peacock (1975a) it is possible to calculate a likely over-estimation of 16% or under-estimation of 14% in elongation rate from Model 1 if the field temperature at 5 cm above the soil surface changes from 15 to 14°C, or *vice versa*, in successive measurement periods. However, over- or under-estimates of the elongation rate brought about by fluctuation in temperature are likely to cancel out during the measurement period of two weeks. Water deficit may introduce bias in the estimate, but severe stress is needed (potential soil water deficit 8-12 cm) for reductions in leaf growth of 0.25 of irrigated swards (Leafe *et al*, 1975).

The effect of leaf age is unlikely to be self-cancelling since elongation rate in all leaves which stop elongation between two observations may be overestimated either by using the elongation in the previous period, or by using the average of the undefoliated actively expanding leaves in the same period. This effect may be offset to some extent by the under-estimation when zero value has to be ascribed because a leaf has been defoliated in two or more successive periods. This obviously will depend on the probability of a leaf stopping growth between two periods and the probability of a young leaf being defoliated two or more times in a fixed period of time (e.g. two weeks).

The adjusted estimation of the elongation rate of an extending leaf is usually averaged on a tiller basis over a period of 15 days, during which five estimates are made (Bircham, 1981b), and thus the effect of the possible bias in the adjusted estimate, or the

effect on the variance introduced by using Model 2, are somewhat diluted when mean rate and variance are calculated in a per period and per tiller basis. Nevertheless, in considering the selection of the model on which to base the correction for defoliated tillers, the likely effect on the treatment mean, or on the variance, may ultimately depend on the frequency with which the adjustments have to be made on elongating leaves. This would depend on the probability of an actively expanding leaf being defoliated once and the probability of the same leaf being defoliated twice or more times in a two-week period. The probability of an actively expanding leaf being defoliated is likely to be high since the animal appears to graze by horizons from the sward surface downwards (Hodgson, 1982) and the youngest leaf is generally located in the upper layers of the canopy (Bircham, 1981b). However, the probability of being defoliated twice in a short period of time may be reduced after the first defoliation since the relative location of a leaf in the canopy is likely to change as a result of having been defoliated (Barthram, 1980).

Alternative models are possible. One alternative is to apply the standard methods to calculate missing values (Cochran and Cox, 1956) and a second is to use a constant rate corrected by the prevailing weather condition during the period between two observations. Using the first approach may reduce the effect on the treatment variance but will not completely remove it. The second alternative is more attractive, but a better understanding of the elongation of leaves in sward conditions and the interactions with the environment would be needed. On the available evidence

Table D1.1 Proportion of actively elongating leaves defoliated at least once (a) or more than twice (b) between two observations (observation separated by 3.5 days) and leaves that apparently stopped elongation between both observations (c). Expt. 3.

Species	Defoliated		Stopped Elongation
	a	b	c
Ryegrass*	0.12	0.02	0.03
Poa†	0.08	0.01	0.04

* over a total of 1350 leaves

† over a total of 1630 leaves

there was no clear basis for choosing either of the main correction models postulated earlier, but evidence drawn from Experiment 3 was used to provide more detail for the assessment. The proportion of the actively expanding leaves defoliated at least once in any one 3.5-day period was calculated from information recorded for ryegrass and *Poa* (Table D1.1). The proportion of leaves that were defoliated was higher for ryegrass than for *Poa*, and this may be expected since young ryegrass leaves tend to be located higher in the sward canopy than are *Poa* leaves (Bircham, 1981b). Overall 0.1 of the expanding leaves present were defoliated in a 3.5-day period, and there would be a risk of bias introduced to the estimation of elongation in these leaves as a consequence of variations in the prevailing weather conditions during the period used to make the estimate. G.T. Barthram (personal communication) has calculated that only 0.03-0.05 of the elongating leaves may be defoliated in swards grazed at comparable herbage mass but with higher tiller population densities. In 0.015 of cases the growth of leaves may be underestimated when a zero value is ascribed because no previous record is available to use in the estimate, but this bias may be counterbalanced by the overestimation in 0.03 of cases where leaves stopped growing between two observations.

These results indicate that the risks of serious bias are very small with either correction model, but suggest that some minor gain in the accuracy of estimates of leaf extension might be gained by using Model 2 instead of Model 1. However, in the present project Model 1 was used for practical reasons and under the assumption that deviations from the mean temperature cancelled out during the measurement period. Short drought periods may have provided another

source of bias, but soil water deficits of 8-12 cm are needed for effects on the extension rate to be important (Leafe *et al*, 1975). The fact that growth-rate estimates over a range of treatments are in good agreement with growth-rate estimations made by other workers within Britain using alternative methods (see discussion by Bircham, 1981b) gives for the time being enough confidence in the accuracy of the technique.

CHAPTER 4

EXPERIMENT 3

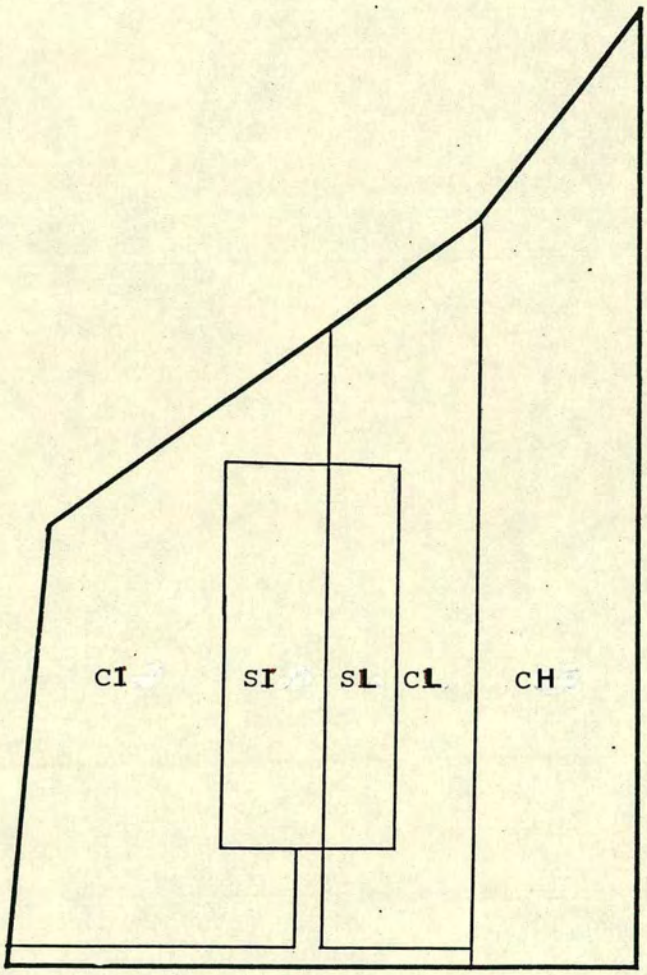


Figure E3.1. The experimental layout for Experiment 3.

GENERAL

This experiment was set up to study the fluxes of plant tissue under cattle or sheep grazing alone in comparable conditions. It was conducted during the summer of 1980 on Met II field (Plate E3.1) of the Hill Farming Research Organisation's Glensaugh Research Station, situated on the eastern edge of the Grampians, Kincardineshire, Scotland.

The field was cultivated and sown with *Lolium perenne* L. cv. Caprice and *Trifolium repens* L. cv. S100 in the spring of 1978. It was cut for silage and the aftermath was grazed by cattle in summer and autumn of 1979. A high proportion of spontaneous *Poa annua* L. was present in May 1980 when the treatments were allocated.

SWARD MANAGEMENT AND EXPERIMENTAL DESIGN

The field was continuously grazed by sheep from April to May at an average height of 3.5 cm. Fertiliser (N = 100 kg ha^{-1}; P_2O_5 = 49 kg ha^{-1}; K_2O = 49 kg ha^{-1}) was applied at the beginning of April and 150 kg N ha^{-1} was applied in three equal dressings of 50 kg ha^{-1} in May, July and August.

By the end of May five paddocks were established and five treatments were allocated without replication (Fig. E3.1). The treatments were the result of a combination of levels of herbage mass, monitored by sward surface height, and two animal species grazing (Table E3.1). The relationship between sward surface height and herbage mass calculated by Bircham (1981) was used to select the treatments.

Table E3.1. Description of the treatments applied to paddocks in Experiment E.3 in May 1980.

Animal Species	Treatments		
Cattle	C L	C I	C H
Sheep	S L	S I	
Intended herbage mass kg OM ha^{-1}	1000	1500	2500
Intended height cm	2.0 - 2.5	3.0 - 3.5	6.0 - 6.5

The paddocks were allowed to grow or were grazed down to the mass required. Once the desired levels of herbage mass (height) had been approximately achieved, the management decision to maintain swards in steady state was controlled by height measurements taken twice weekly and stock numbers adjusted immediately.

ANIMALS

Mature Greyface ewes with single lambs and yearling female Friesian cattle were weighed (non-fasted) and allocated to treatments at initially similar average live weights within animal species. Similar heifers fistulated at the oesophagus in March and ewes fistulated the year before were grazed together with non-fistulated animals. The ewes were sheared in July and the lambs were weaned in August. All animals were drenched with the propriety anthelmintic.

SWARD MEASUREMENTS

Estimations of the above-ground herbage mass and sward surface height were made regularly throughout the season on all swards. Detailed descriptions of the vertical distribution of the dry matter and canopy structure were made on three occasions, at the same time as the detailed observations on tissue fluxes. These detailed

measurements were conducted in the two-week periods 26 June-11 July, 4-20 August and 10-25 September which will be described henceforth as Period 1, Period 2 and Period 3 respectively. These detailed observations consisted of linear and leaf area measurements on grass tillers and clover stolons. Measurements of herbage intake (Hodgson and Rodriguez Capriles, 1970) and of the diet selected were made at the same time.

Herbage Mass

The paddocks were divided transversely into quarters for all sward measurements, and one quarter of the total number of samples referred to in the text were taken from each notional division.

Sixteen quadrats of 1.22 m x 0.15 m were cut every two weeks at ground level, using Sunbeam Shearmaster shearing hand pieces. Additional samples 0.20 m by 0.20 m were taken at each quadrat site, placed in self-seal plastic bags and frozen and stored at -20^{o}C, to estimate the botanical and morphological composition of the swards. The quadrat samples were dried at 80^{o}C for 12 hrs, weighed individually and bulked on an operator basis for determination of the ash content.

Sward height

The surface height of the sward was measured twice a week using a graduated stick with a perspex slide (Bircham, 1981). The perspex slide was lowered until the first contact on undisturbed foliage was made, and the height of this point from the soil surface was recorded.

Forty observations per paddock (twenty pairs) were used to estimate the average height of the sward surface. This mean height was used to monitor the "steady-state" of the swards. The functional

relationship between sward height and herbage mass calculated by Bircham (1981b) for similar swards grazed by sheep was used to predict the sward surface height required to achieve desired levels of herbage mass in this experiment.

Population density

The population densities of *Poa* and ryegrass tillers, clover active meristematic points, weed stems and dead shoots were estimated once in every detailed observation period. An additional estimation was made at the beginning of the next grazing season, during the first week of April 1981. Twenty 0.20 m x 0.20 m turf samples were taken to the laboratory and subsamples of 0.10 m x 0.05 m were harvested. All visible daughter tillers bearing more than one leaf were counted. An active meristematic point for clover was defined as an aggregation of two or more petioles associated with active stolon formation.

Vertical Distribution of the Herbage Mass

The vertical distribution of the herbage mass was estimated on a total species basis by sampling in horizons 2 cm deep from quadrats of 0.10 m x 0.05 m in the laboratory. Eight turves similar in size to those taken for population density estimations were taken from the field. The samples were harvested using hand shears and a guide device to determine the horizon depth (Plate E3.2). Each horizon was separated into live ryegrass, *Poa*, clover, dead , attached and detached and seed head. The components were dried at 80°C for 12 hrs and then weighed, and samples from the 0-2 cm horizon were washed in water before drying.

Canopy Geometry

Two 0.20 m x 0.20 m x 0.10 m turf cores were taken from the field to the laboratory in order to describe the canopy structure. Five tillers/growing points per species were selected by a vertical point, first hit method and the height of the tops of all laminae and petioles and the height of the ligule or petiole insertion was measured. The length of the pseudostem or stolon and the height of insertion of the penultimate youngest leaf in grasses or the ultimate leaf in clover was measured. All these measurements were made using a graduated dissection needle to avoid disturbance of the sward canopy.

Sward Profile Description

Four transects 25 m long were permanently marked with two wooden pegs. The transects were defined by choosing the co-ordinates of a base point and the angle of the projection at random. The surface height of the sward canopy was measured at 0.10 m intervals along each transect before and after the second and third detailed observation periods. The canopy height was measured using a vertical graduated shaft and a plastic disc (1.8 g and 3 cm diameter) which settled on the herbage. The height from the disc to ground level was recorded in cm.

In each quarter of a paddock one dung pat was chosen at random and a short transect of 70 cm length was set up from the centre of each patch. The alignment of each transect was also chosen at random but possibilities where the transect would have been influenced by another patch were disregarded. Sward height measurements were recorded in 5 cm intervals along these transects using the same device as in the long transects.

Table E3.2. Height used to determine borders between least grazed, intermediate and most grazed zones (cm) from Huber (personal communication)

Zone[+]	Treatments				
	SL	SI	CL	CI	CH
I	> 4.0	> 5.5	> 4.0	> 9.0	> 9.0
II	3.0-4.0	4.0-5.5	3.0-4.0	4.5-9.0	6.0-9.0
III	0.0-3.0	0.0-4.0	0.0-4.0	0.0-4.5	0.0-6.0

[+] I least grazed zone

II intermediate zone

III most grazed zone

For estimates of the area partially grazed in the whole paddock the herbage along each transect was defined, as objectively as possible, in three zones: an ungrazed zone close to the dung pat, a grazed zone at the distal end of the transect similar to the surrounding grazed sward, and an intermediate zone. The herbage height where one zone changed into another was then derived from the highest or lowest value on either side of the zones marked in the chosen transects. The herbage heights so established are shown in Table E3.2. The frequencies of herbage heights on the long transects equivalent to each zone were expressed as a proportion of the total observations made and these were taken as estimates of the relative proportions of each zone in each paddock (A. Huber, personal communication).

Tissue Turnover Estimations

Measurements of the lengths of green laminae and pseudostems on individual tillers (Bircham, 1981b; Davies, 1981) were made on five successive occasions at 3 and 4 day intervals during each detailed observation period. Petiole and stolon length was measured in clover on the same occasions. Leaf Area and weight per unit area were estimated from dissected tillers which were selected at random from each sward, and used to convert within-sward linear estimations into weight estimates.

Forty tillers or growing points per species were marked in each paddock along eight transects of five units per species, in order to help to locate the marked units. Each transect was defined as a line of 1.5 m between two pegs. The transects were allocated at random in each quarter of a paddock and tillers or

growing points were chosen at intervals of 0.1 m. At each point a tiller or a growing point was chosen on a vertical first-hit basis. The unit was identified with a plastic wire ring anchored to the soil with a flat-head nail of 0.12 m length. All the units lost by grazing activities or other causes were replaced by a new unit. Linear measurements were made on 600 individuals, 40 per species per paddock. A new set of units was marked for each of the three detailed observation periods.

Linear measurements

The procedures used have been recently described by Bircham (1981b) and Davies (1981). The leaves were numbered from the bottom to the top of a tiller in grasses and from the distal leaf to the active bud in clover.

Grasses

The length of all green laminae from the ligule to the tip or the edge of the yellow region was measured. If the dead tissue was irregularly distributed e.g. as a consequence of fungal attack, an estimate of the length of green tissue was made. The length of the pseudostem from the ligule of the penultimate youngest leaf to the ground was also recorded. All the flowering stems were measured from the ligule of the flag leaf to the tip of the flower head. All laminae of new tillers were recorded as a single morphological unit, and no pseudostem records of these tillers were made. The total number of secondary tillers per marked tiller was also recorded.

On the first recording day and thereafter each lamina was described as defoliated or not. Defoliated leaves were identified with a slit made with the tip of a metal rule used in the measurements

(Plate E3.3) and if the slit was absent at the subsequent observation, the lamina was recorded as having been defoliated in the preceding interval. Defoliation of an initially entire lamina was recognised when the tip was absent.

White clover

Similar techniques were used to do the linear measurement in white clover. Because of the irregular shape of white clover leaves, a functional relationship between petiole length and estimated potential lamina area, (Williams, Evans and Ludwig, 1964) corrected by planimeter determination of the lamina area was calculated (Bircham, 1981b). The length of the petiole from the insertion in the stolon to the lamina base, and stolon length from the distal end of a growing point to the stipules of the terminal leaf were recorded. All secondary branches per marked unit were recorded, but only one, the second numbering from the terminal leaf, was measured, and it was assumed to be representative of the other daughter branches (Bircham 1981b). As in grasses each leaf at the initial observation and thereafter was recorded as defoliated or not. The proportion of lamina absent was estimated visually to the nearest third of a leaflet. This approximation was found precise enough to enable recognition of defoliation occurring between two subsequent observations. The information was directly recorded onto computer forms by two teams of two persons, one measuring and one recording.

Auxilliary Measurements

Leaf Area

The areas of individual grass laminae (16 lamina per treatment) were estimated from mid-rib lamina length (L) and its breadth one

half of the way along its length (B 0.5) (Robson and Sheehy, 1981), and from direct planimetric measurements using an electronic planimeter. A functional relationship between these two estimations of leaf area was established by linear regression using planimeter area estimations as the dependent variable and area estimated by L and B 0.5 as the independent variable. One equation was calculated for each grass species with plants collected in each detailed observation period (Table E3.3). A similar relationship was established for white clover but the independent variable was an estimation of the leaf area by the superimposition of the leaf on a set of patterns arranged in a logarithmic scale (Williams, Evans and Ludwig, 1964). The leaves were matched with the potential pattern (i.e. entire leaf) and the absent portion of any one leaf was estimated visually as described before, and discounted from the potential area. A linear regression between both estimations of the area was calculated with material collected in each detailed observation period (Table E3.3).

Petiole Length to Lamina Area Relationship

The functional relationship of the length of the petiole and the potential area (all the leaflets intact) corrected by planimeter estimations of one hundred clover leaves was established for each period. The potential lamina area was used as the dependent variable and the petiole length as the independent variable. The equations derived given in Table E3.4, were selected on the best fit base between a linear and power model (Bircham, 1981).

Lamina, Petiole, Pseudostem and Stolon Weights

Ten tillers per grass species per treatment were dissected in the laboratory and B 0.5 and L for each laminae and the length of the pseudostem were recorded. The leaves of the ten tillers were bulked according to two categories (i.e. leaf currently in expansion, and fully expanded leaves) and oven dried for 12 hrs at $80^{o}C$ and weighed. The procedure for clover was similar except that only one category was recognised (expanded leaves) and petiole length and lamina area were estimated as described before.

Net Canopy Photosynthesis

Eight turves (0.25× 0.25 × 0.10 m) per paddock were brought to the laboratory during each detailed observation period. Net canopy photosynthesis estimates of the entire sward at 320 $W\,m^{-2}$ of photosynthetically active radiation were made as described by King *et al* (1979).

ANIMAL MEASUREMENTS

Live Weight

All ewes, lambs and heifers were weighed weekly (non-fasted) throughout the experiment using a fixed weighing crate.

Herbage Intake

Herbage intake in ewes, lambs and heifers was calculated from estimation of faecal output and the organic matter digestibility of the diet selected (Hodgson and Rodriguez Capriles, 1970).

Faecal Output

Faecal output was estimated using chromium sesquioxide (Cr_2O_3) as indigestible marker (Hodgson and Rodriguez Capriles, 1970). Five pairs of ewes and lambs (four ewes only in period three) and five heifers per treatment were dosed with pellets of shredded paper

impregnated with chromic oxide (Corbett, Greenhalgh and MacDonald, 1958). Doses of pellets weighing 3 g, 1 g and 0.5 g (approximately 24% Cr) were given to heifers, ewes and lambs twice daily for twelve days. At the time of dosing (0830 hrs and 1630 hrs) on the last five days of each period, a faecal sample was taken from the rectum of each animal and frozen and stored at -20°C until the end of the experiment. Faecal samples were bulked on an individual animal basis, freeze dried and ground for ash and chromium determination.

A modification of the technique described by Williams, David and Iismaa (1962) utilising atomic absorption spectrophotometry was used for determination of chromium in pellets and faeces.

Organic matter digestibility

The digestibility of the diet selected was estimated from samples of extrusa collected by oesophageal-fistulated animals during each detailed observation period. All fistulated ewes had been used in previous experiments, the heifers were fistulated before the experiment started. Four ewes were alternated in pairs between the two treatments in each period and were sampled once a day, while three heifers were rotated round the three treatments singly and were sampled in the morning and in the afternoon of the same day. The animals were penned for approximately two hours prior to sample collection. The samples were frozen and stored at -20°C until the end of the experiment. The frozen extrusa samples were broken up and divided in two sub-samples, one of which was freeze dried and analysed for organic matter digestibility (OMD) (Alexander and McGowan, 1966). The second half was stored frozen for subsequent botanical analyses.

Botanical composition of the diet selected

The extrusa samples selected by ewes and heifers was separated into live and dead material of the following components: grass laminae, pseudostem, reproductive grass stem, grass seed head, clover laminae, clover petiole and clover stolon, weeds, moss and roots.

The components were manually separated from sub-samples handled in petri dishes illuminated from beneath. The separated components were oven dried at 80°C for 24 hrs and then weighed. The remainder of the sample was bulked on a sward basis. The same components, although with grass lamina identified to a species level, were determined in three sub-samples per treatment by binocular observation (Heady and Torell, 1959).

Grazing time

Four heifers and six ewes per treatment were fitted with Kienzle Vibracorders (Allden, 1962; Stobbs, 1970) during the second and the last week in August and again the first and the third week in September. Vibracorder charts were replaced at 1000 hrs on each morning during five consecutive days.

Intermediate calculations and statistical analysis

Tissue turnover calculation

Tissue changes per leaf (positive and negative) were calculated as the difference in the green length of the laminae between two observations from equation E3.1.

$$T = (GLL)_{t_1} - (GLL)_{t_o} \qquad \text{e.q. E3.1}$$

where T = tissue change; GLL = green laminae length and t_1 and t_o = observation times.

The numbers of leaves growing, senescing and in steady state per tiller were identified from the field codes in order to integrate leaf changes on a tiller basis. Net change was calculated by difference between positive (elongation) and negative (senescence) changes. If a leaf was defoliated in the interval between two observations, the leaf elongation rate was assumed to be the same as in the previous interval. If no estimate of leaf elongation rate could be obtained because the leaf had been defoliated in the previous interval also, zero increment was assumed.

The linear measurements (page 77) were first transformed into area and then transformed into weight. The area transformation in grasses was done by multiplying laminae length values measured in the field by B 0.5 of the given leaf category (see page 79) and corrected by the equation relating planimetric area estimation to L x B 0.5 area estimation (Table E3.3). The B 0.5 of the laminae for the youngest leaf was used for daughter tillers.

The area transformation for white clover was made by using the equation calculated for petiole length and potential laminae area from the empirical logarithmic scale (Table E3.4). This value was then corrected by the equation relating the empirical estimation with the planimetric estimation of the leaf area. This potential estimation of the area (i.e. three intact leaflets) was then corrected by actual proportions estimated visually in the field (see page 81). The mean laminae weight per unit area per leaf category (see page 82) and mean pseudostem, mean stolon and mean flower head weight per unit length, were used to convert area and length observations into weight.

The changes were integrated on a locus basis (parent unit + daughter units) and then were integrated on a species per unit area basis, and, by summing across the species, on a paddock per unit area basis. The locus changes were converted into rates of change per species per unit area by transforming locus observations into single units and then multiplying by density per species (Equation E3.2).

$$A = LxTd \times \frac{1}{1+D} \qquad \text{e.q. E3.2}$$

where A = increment per species.ha^{-1}; L = increment per locus; Td = tiller/growing points density, estimated according to page 73 ; and D = secondary units (average for the period).

Rates of tiller appearance and disappearance were calculated from the tillers marked for tissue turnover. These correspond to the gross tiller appearance (TAR) and death rates described by Thomas (1980) over periods of 14 days.

Tiller death rate is renamed here as disappearance rate since it was not possible to confirm death on all disappeared tillers.

In calculating frequency of defoliation, a negative bionomial distribution was assumed (Fenlon, 1978; Fenlon, personal communication) i.e. the number of observations until the first defoliation occurred was used instead of the number of times a tiller was recorded as defoliated in a fixed number of observations (Hodgson, 1966; Hodgson and Ollerenshaw, 1969). The calculations were carried out using a series of Fortran IV routines (Bircham 1981b) implemented on an ICL 2980 Computer.

Herbage intake calculation

Faecal organic matter output was calculated from chromium content

in faeces and pellets, and from faeces ash content from equation E3.3.

$$FOMO = 2 \times \frac{CPC}{CFC} \times (100 - FA) \qquad \text{e.q. E3.3}$$

where FOMO = faecal organic matter output(g); CPC = chromium pellet content (g); CFC = chromium faecal content (gg^{-1}) and FA = ash content in faeces (proportion). Organic matter intake was calculated from faecal output and digestibility as in equation E3.4.

$$OMI = FOMO \times \frac{100}{100-OMD} \qquad \text{e.q. E3.4}$$

where OMI = organic matter intake(g); FOMO = faecal output of organic matter (g) and OMD = organic matter digestibility.

The calculations were performed by a Fortran IV routine implemented on an ICL 2980 Computer.

Statistical analyses

The pooled standard error of the difference (SED) for treatment mean comparisons was calculated by analyses of variance (ANOVA). The sward data were classified in a nested fashion in time, paddocks, plant species, quarter of a paddock, transects and tiller classes. Quarters of a paddock, transects and tiller classes were included in order to estimate within-treatment variance.

The treatments sum of squares was partitioned into four comparisons among treatments effects, with one degree of freedom for each comparison: the two main effects, herbage mass and animal species, their interaction, and the high herbage mass grazed by cattle against the average of the other treatment effects were specified for all the variates under investigation.

Although the distribution of some variables was skewed, no transformations were made on the data and it was assumed that the

Table E3.5. Example of analysis of variance carried out on the per species performance per unit of area.

SOURCE OF VARIATION	DF
PQ Stratum	
Paddocks	4
Low vs intermediate herbage mass	1
Interaction mass x animal sp.	1
Cattle vs sheep	1
High herbage mass vs low and intermediate	1
RESIDUAL	15
TOTAL	19
PQ[+].TRANCTQ[*] STRATUM	
• SPE	2
PADDOCKS.SPE	8
RESIDUAL	90
TOTAL	100
PQ.TRANCTQ.TILLERS STRATUM	480
PQ.TIME STRATUM	
TIME	2
PADDOCKS.TIME	8
RESIDUAL	30
TOTAL	40
PQ.TRANCTQ.TIME STRATUM	
SPE.TIME	4
PADDOCKS.SPE.TIME	16
RESIDUAL	180
TOTAL	200
PQ.TRANCTQ.TILLERS.TIME STRATUM	960
GRAND TOTAL	1799

[+]PQ = paddocks quarters

*TRANCTQ = transects within quarters

• SPE = plant species

analysis of variance technique was robust enough to cope with small departures from normality. Because there was no replication of sward treatments, it was problematic how to estimate the residual variance for paddocks comparisons. It was decided that the paddocks x quarter interaction would be the most appropriate mean square in the absence of replicates, since a quarter was the most homogeneous block to which the treatments were applied (see Table E3.5).

The herbage intake, diet botanical composition, diet digestibility and grazing time treatment means were compared by estimating SED by standard ANOVA techniques. The total herbage consumed per hectare was calculated by multiplying the intake of each animal by the stocking rate calculated for the particular period.

All the analyses of variance were carried out using a statistical package GENSTAT version 4.03 as implemented by Edinburgh Regional Computing Centre.

RESULTS

INTRODUCTION

In this section mean treatment effects are presented as Tables or block diagrams. When mean effects are presented as diagrams, the tables with the actual values and standard errors of the mean are given in Appendix A3 in the same sequence.

Herbage mass and sward surface height

Herbage mass (kg.OM ha^{-1}) and sward surface height (cm) in the five paddocks for the three periods are given in Table E3.6. Herbage mass was greatest in period 1 and then declined towards the end of the season (2800; 1900; 1600 ± 71 kg.OM ha^{-1}, $P < 0.05$).

However, overall, the desired contrasts between mass levels within animal species were achieved (3100 vs 2100 vs 1700 ± 64 kg OM ha^{-1}, $P < 0.05$) and differences between animal species were not significant. Sward surface height was held within the specified ranges, although the time x paddocks interaction was significant.

The pooled linear regression of the average herbage mass per quarter plot (HM) on sward surface height (SSH) was significant ($P < 0.05$) but, it only accounted for 27% of the variance (Equation E3.5).

$$HM = 328.4\ (\pm\ 49.2) \times SSH + 943.7\ (\pm\ 186.6) \qquad n = 120 \qquad \text{e.q. E3.5}$$

The relation was greatly improved ($P < 0.05$) by assuming parallel regressions within individual periods (Equation E3.6).

$$HM = 359.6\ (\pm\ 33.4)\ SSH + \begin{matrix}(1568.6\ (\pm 149.1) \\ (\ 702.0\ (\pm 113.4) \\ (\ 238.1\ (\pm 113.8)\end{matrix} \qquad \text{e.q. E3.6}$$

n = 40, percentage variance accounted for by regression 67.

Sward Profile Description

In order to compare the components of the variance of sward surface height between animal species and between periods of time a generalised linear model was fitted to the within-plot variances of the height measurements recorded along the fixed 25 m long transects (page 74). As the residual variance was too great to accept the model and test the deviance against a X^2 (Baker and Nelder, 1978) the treatment effects on the variances were tested against an ordinary F.

The mean variances per treatment for Period 2 and Period 3 are given in Table E3.7. The interaction period x paddocks was

significant ($P < 0.05$). In Period 2, the variance of the sward surface height increased proportionately to herbage mass, but the increment was higher in cattle- than in sheep-grazed swards. However, by the end of the experiment only the variance at the high level of mass differed from the average of all the other treatments.

Table E3.7. Mean of the sward surface height variance for swards grazed by sheep or by cattle (cm^2).

Treatment	Period 2	Period 3
SL	8.6	5.8
SI	19.5	14.4
CL	10.0	14.8
CI	46.3	13.7
CH	204.8	87.5
$SE\bar{x}$		3.66

Relative areas with different degrees of utilisation

The proportion of areas at different degrees of utilisation on the whole paddock calculated as described in page 76 are given in Table E3.8.(A. Huber, personal communication). The way data were calculated did not allow any statistical analysis.

Table E3.8. Estimated area of each zone in percentage of the whole paddock from A. Huber (personal communication)

Zone†	Treatment SL	SI	CL	CI	CH
I	0.12	0.10	0.08	0.03	0.16
II	0.21	0.23	0.12	0.13	0.24
III	0.67	0.67	0.80	0.84	0.60

† I = least grazed zone
II = intermediate zone
III = most grazed zone

Sward botanical composition

Samples taken as described in page 71 were bulked per quarter base and separated into the following components per plant species: lamina, pseudostem (stolon) and total dead, attached and detached dead roots; and weeds.

Total live lamina, ryegrass and *Poa* live lamina, detached and attached dead and total pseudostem as a proportion of the total mass for the five treatments and three periods are given in Table E3.9.

The proportion of total lamina was not affected by animal species but it increased as herbage mass increased. Ryegrass and *Poa* lamina proportions were similar at low herbage mass and the proportion of ryegrass lamina increased as herbage mass increased. The clover lamina contribution ranged only between 0 and 0.05. Dead attached and dead detached were not clearly affected by either herbage mass or animal species but the interaction mass x animal species was significant ($P< 0.05$); both components increased

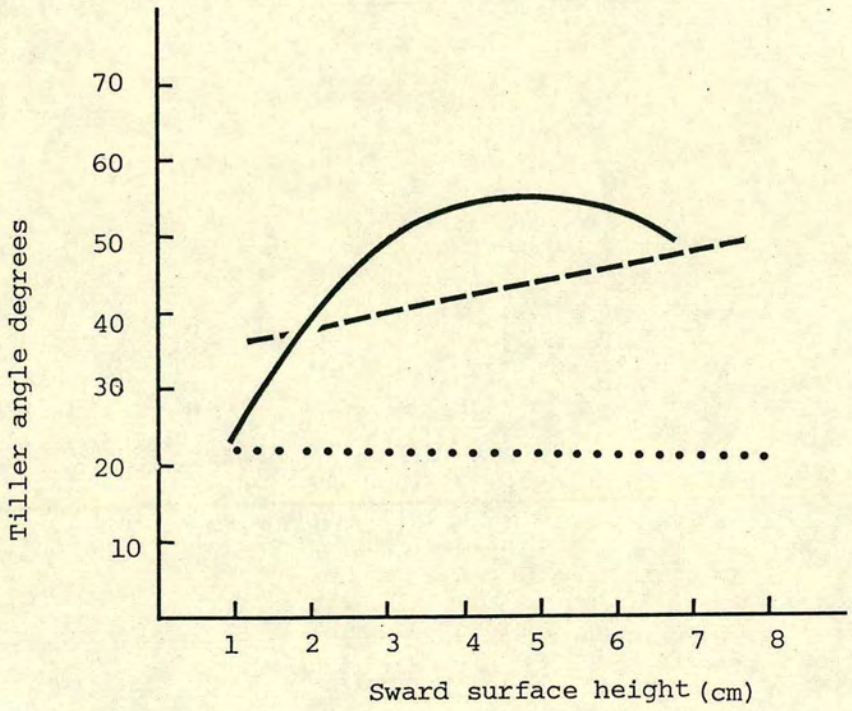


Figure E3.8. The relationships between tiller angle (angle which size = pseudostem/height of the ligule of the second youngest leaf) for ryegrass (——), Poa (– – –) and white clover (••••).

were located higher in the canopy than those of *Poa* and the youngest clover petiole lay close to the ground, the differences between grasses increasing with the height of the sward surface.

The tips of the second youngest ryegrass and *Poa* laminae were at the same height in the canopy and over topped the second youngest clover petiole at all sward surface heights (Figure E3.6b). The same pattern was observed in the height of the ligule of the penultimate youngest leaf, in pseudostem or stolon length and in tiller angle, the exception being ryegrass tiller angle where a quadratic relationship gave the best fit (Figure E3.7a and b and Figure E3.8). The sine of the tiller angle was calculated from the height of the ligule of the penultimate youngest leaf (stipules) divided by pseudostem (stolon) length. None of the components of canopy geometry was affected by animal species grazing (Tables A3.2, A3.3 and A3.4, Appendix A3). All the regression equations used in this section are given in Table A3.5, Appendix A3.

Species Population Density

Mean species and total population densities for the three experimental periods and for April 1981 are given in Figure E3.9 and Table A3.6 (Appendix A3). In the total and in the ryegrass and *Poa* populations, the two-factor period x paddock interaction was significant ($P< 0.05$). The total population was higher at the low than at the intermediate herbage mass in sheep-grazed swards but it was not affected by herbage mass in cattle-grazed swards. By September the total population was higher at the low herbage mass than at the intermediate herbage mass (28800 vs 24500 ± 1400 tillers m^{-2}, $P< 0.05$) but this effect was reversed during the winter

(23900 vs 27700 ± 1400 tillers.m^{-2}, $P < 0.05$). On the other hand total population density was higher in sheep- than in cattle-grazed swards throughout the experiment period (28300 vs 21500 ± 1040 tillers.m^{-2}, $P < 0.05$) and this difference persisted until the following spring (28700 vs 22900 ± 1400 tillers.m^{-2}, $P < 0.05$).

Overall *Poa* population was the highest followed by ryegrass and then white clover (13600 vs 9300 vs 800 ± 900 tillers.m^{-2}, $P < 0.05$). Overall for both ryegrass and *Poa* components, density was higher in sheep- than in cattle-grazed swards (11200 vs 7400 ± 600 and 16500 vs 13500 ± 700 tillers.m^{-2}, $P < 0.05$) and *Poa* density was higher at the low than at the intermediate herbage mass (16300 vs 13700 ± 700 tillers.m^{-2}, $P < 0.05$). The clover component was less than 3% of the total population in all treatments, and there were no significant effects either of period or animal species or herbage mass.

Tiller turnover

The rates of change in tiller population densities were derived from the marked tillers and stolons (see page 86) and are quoted as relative rates (tillers.100 tillers^{-1}.day^{-1}).

Analysis of variance was carried out on the rates of tiller appearance, disappearance and net change transformed to logarithms as well as on the untransformed data. The transformation of the data was decided in view of the non-linear relationship between means and variances. However, as it is possible to draw similar conclusions from both analyses, the untransformed data are used here and are depicted in Figure E3.10a, b and c and Tables A3.7, A3.8 and A3.9 (Appendix A3) for each plant species respectively. The two-factor period x plant species interaction was significant ($P< 0.05$)

for appearance rate, the paddock x plant species for disappearance and net appearance rates and the paddock x period for disappearance rate were also significant ($P < 0.05$). However, overall the three rates were higher in June-July and they decreased towards the end of the season, and rate of appearance and net change were higher in *Poa* and clover than in ryegrass.

The rate of tiller appearance in both ryegrass and *Poa* was higher at the low than at the intermediate herbage mass ($P < 0.05$), although this effect was less marked at the end than at the beginning of the experiment. The appearance rates at the high and intermediate herbage masses grazed by cattle were similar although in *Poa* the rate was very low at the end of the season.

The rate of tiller disappearance followed a similar pattern in both grasses, i.e. it was higher in cattle- than in sheep-grazed swards ($P < 0.05$) and higher at the low than at the intermediate mass ($P < 0.05$). However, both herbage mass and kind of animal effects were less marked in *Poa* than in ryegrass, and the differences due to herbage mass were smaller at the end of the season.

The rate of net change in tiller density was higher in *Poa* than in ryegrass but the pattern was similar in both species, the rate being higher in sheep- than in cattle-grazed swards ($P < 0.05$) and higher at the low than at the intermediate mass ($P < 0.05$). However, in *Poa* the high rate at the low herbage mass grazed by sheep made the interaction mass x animal species significant ($P < 0.05$).

The clover active meristematic sites appearance rate was not affected by herbage mass or animal species, although in August the rate was higher at the low than at the intermediate herbage mass ($P < 0.05$).

The disappearance rate of clover active meristem was higher at the low than at the intermediate herbage mass ($P < 0.05$) and the rate of net change was higher at the intermediate than at the low herbage mass ($P < 0.05$). At the beginning of the experiment net change was higher at intermediate than at lower herbage mass but this effect disappeared late in the season.

All the rates at the high herbage mass grazed by cattle were similar to the rates at the intermediate herbage mass grazed by cattle.

Frequency of defoliation

The frequency of defoliation of individual tillers (no.defoliation.day^{-1}) for the five treatments and for the three periods is given in Table E3.10 for ryegrass,*Poa* and white clover. The three factors period x plant species x paddocks and all the two-factor interactions were significant ($P < 0.05$). However, overall the frequency of defoliation was higher for ryegrass and white clover than for *Poa* (0.12 vs 0.09 vs 0.12 ± 0.002 defoliations.day^{-1}, $P < 0.05$), and in periods 1 and 2 than in period 3 (0.12 vs 0.12 vs 0.09 ± 0.002 defoliations.day^{-1}, $P < 0.05$). Over all three periods, the frequency of defoliation was highest at low herbage mass (0.12 vs 0.11 ± 0.002 defoliations.day^{-1}, $P < 0.05$). On average the sheep grazed individual units more frequently than cattle (0.12 vs 0.11 ± 0.002 defoliations.day^{-1}, $P < 0.05$). The frequency of defoliation at the high herbage mass was similar to the frequency at the intermediate herbage mass. The intervals between defoliations (the inverse of defoliation frequency) are given in Table A3.11, Appendix A3.

Tissue turnover

The rates of gross growth, senescence and net growth are all

presented at different levels of detail; per primary units, plant species per unit area and total sward per unit area. Primary unit refers to a tiller or active meristem marked as an apparently independent unit and does not include any visible daughter tiller or branch. Plant species per unit area is calculated as indicated in page 84 and the total sward per unit area is the sum of the three plant species per unit area.

Total growth, lamina senescence and net growth rates per primary unit ($\mu g.unit^{-1}.day^{-1}$) for the three experimental periods are depicted in Figures E3.11a,b and c and Tables A3.11, A3.12 and A3.13 for ryegrass, *Poa* and white clover respectively. For all rates the three-factor period x plant species x paddocks interaction was significant ($P < 0.05$) as well as all the two-factor interactions. However, all the rates were highest in white clover followed by ryegrass and *Poa*, and they were highest in period 2.

Overall total growth and lamina senescence rates per primary unit in ryegrass and *Poa* were not affected by kind of animal but the interaction on animal species x herbage mass was significant ($P < 0.05$) for ryegrass growth rate in period 2. On the other hand, ryegrass growth and senescence rates were higher at intermediate than at low herbage mass (371.8 vs 239.0 ± 23.3 $\mu g.unit^{-1}.day^{-1}$, and 188.7 vs 116.1 ± 17.5 $\mu g.unit^{-1}.day^{-1}$ growth and senescence respectively, $P < 0.05$) and although the same pattern was observed in *Poa*, the differences were not significant. Net growth was not affected by either herbage mass or animal species in either *Poa* or ryegrass.

The rates of gross growth, senescence and net growth at the high mass grazed by cattle were all comparable to the rates at the

intermediate herbage mass grazed by cattle.

Clover growth rate was higher in cattle- than in sheep-grazed swards (757.3 vs 510.1 ± 23.3 µg active meristem^{-1}.day^{-1}, $P < 0.05$) and it was higher at the intermediate than at the low herbage mass (674 vs 592.5 ± 23.3 µg active meristem^{-1}.day^{-1}, $P < 0.05$). However, in periods 1 and 3 the interaction herbage mass/animal species was significant ($P < 0.05$).

The rate of lamina senescence did not follow any clear pattern and the unexpected high rate at the low herbage mass grazed by cattle in period 3 was responsible for the mass/animal species interaction being significant ($P < 0.05$). Net growth rate followed the same pattern as growth rate (494.5 vs 386.3 ± 20.2 µg. active meristem^{-1}.day^{-1}, $P < 0.05$) but differences between herbage masses were not significant. Growth and net production rates at the high herbage mass grazed by cattle were higher than at the intermediate herbage mass grazed by cattle.

Plant species performance per unit area

Total growth, lamina senescence and net production per unit area (kg.DM.ha^{-1}.day^{-1}) are given in Figure E3.12a, b and c and Tables A3.14, A3.15 and A3.16 for ryegrass, *Poa* and white clover respectively. For total growth rate the three-factor period x plant species x paddocks interaction was significant ($P < 0.05$) and for any rate all the two-factor interactions were significant ($P < 0.05$) except the paddocks x period interaction. The three rates in ryegrass and *Poa* were of the same magnitude but in white clover they were usually substantially lower.

Both ryegrass and *Poa* growth rates became progressively higher in sheep- than in cattle-grazed swards and the differences for

ryegrass were significant by the end of the season (32.7 vs 20.3 ± 3.24 kg.dm.ha^{-1}.day^{-1}, $P < 0.05$). Differences due to herbage mass, on the other hand, developed earlier than those due to animal species; growth rate was higher at the intermediate than at the low herbage mass in periods 1 and 2, but by the end of the season the effect had disappeared.

The rate of lamina senescence for both grasses was progressively higher in sheep- than in cattle-grazed swards and this effect was developed earlier in ryegrass than in *Poa*, but by the end of the season the differences were significant in both ryegrass and *Poa* (15.5 vs 10.4 and 14.8 vs 11.1 ± 1.0 kg.dm.ha^{-1}.day^{-1}, $P < 0.05$).

Ryegrass senescence rate over the three periods was higher at the intermediate than at the low herbage mass (15.0 vs 9.0 ± 1.0 kg.dm.ha^{-1}, $P < 0.05$), but *Poa* senescence rate was not affected by herbage mass.

Ryegrass net production over all the three periods was higher in sheep- than in cattle-grazed swards (17.9 vs 12.5 ± 1.7 kg.dm.ha^{-1}.day^{-1}, $P < 0.05$) and it was higher at the intermediate than at the low herbage mass (18.0 vs 12.4 ± 1.7 kg.dm.ha^{-1}.day^{-1}, $P < 0.05$). However, *Poa* net production was not affected either by animal species or herbage mass.

The growth and senescence rates at the high herbage mass grazed by cattle were similar to those at the intermediate mass, but *Poa* net production at the high herbage mass declined significantly towards the end of the season.

Clover rates did not follow a clear pattern and by the end of the season net production was lower than 6 kg.dm.ha^{-1}.day^{-1} in all paddocks.

Combined species performance

Total growth, lamina senescence and net production rates ($kg.dm.ha^{-1}.day^{-1}$) for the three periods are given in Figure E3.13 and Table A3.17. Overall total growth rate was higher in period 2 than in periods 1 and 3 (79.6 vs 54.5 vs 48.5 ± 4.2 $kg.dm.ha^{-1}.day^{-1}$, $P < 0.05$ for periods 2, 3 and 1 respectively) and it was higher in sheep- than in cattle-grazed swards (64.1 vs 53.8 ± 3.3 $kg.dm.ha^{-1}.day^{-1}$, $P < 0.05$). It was higher at the intermediate than at the low herbage mass (66.4 vs 51.4 ± 3.3 $kg.dm.ha^{-1}.day^{-1}$, $P < 0.05$), and the high herbage mass grazed by cattle was not different from the average of the other treatments.

The rate of senescence increased towards the end of the season (18.6 vs 32.2 vs 30.8 ± 2.2 $kg.dm.ha^{-1}.day^{-1}$, $P < 0.05$ for periods 1, 2 and 3 respectively) and it was higher at the intermediate than at the low herbage mass (28.2 vs 22.6 ± 1.6 $kg.dm.ha^{-1}.day^{-1}$, $P < 0.05$) and in turn it was higher at the high herbage mass than the average of the other treatments (34.4 vs 25.4 ± 1.6 $kg.dm.ha^{-1}.day^{-1}$, $P < 0.05$).

Net production followed a similar pattern to total growth, it was higher at the intermediate than at the low herbage mass (38.1 vs 28.8 ± 3.6 $kg.dm.ha^{-1}$, $P < 0.05$) but the overall effect of animal species was not significant.

Canopy net photosynthesis

Estimates of net canopy photosynthesis (320 Wm^{-2}) per unit of LAI for the five treatments and the three periods are summarised in Table E3.11. Net photosynthesis per unit of LAI was higher at the end of the season (1.7 vs 1.7 vs 2.3 ± 0.18 $g.m^{-2}.h^{-1}.LAI^{-1}$ CO_2 at 320 Wm^{-2}, $P < 0.05$). Overall the net canopy photosynthesis

Table E3.12. Leaf area index in swards grazed by cattle or by sheep from May to September 1980.

Treatment/Period	June-July	August	September
SL	1.5	1.4	1.4
SI	2.6	2.7	2.1
CL	1.5	2.4	1.1
CI	2.3	2.8	2.1
CH	3.6	3.3	2.9
$SE\bar{x}$			0.36

Table E3.13. Weight per unit area of immature and of mature leaves ($\mu g\ mm^{-2}$) for ryegrass, Poa and white clover

	Immature		Mature		
Treatment/Leaf	Ryegrass	Poa	Ryegrass	Poa	Clover
SL	45.1	49.5	34.4	33.7	36.1
SI	40.2	28.6	34.8	27.3	31.0
CL	38.1	34.2	34.8	30.9	39.0
CI	55.9	47.1	36.5	31.1	30.4
CH	49.4	41.0	32.0	27.9	33.0
$SE\bar{x}$		5.8			4.45

per unit of LAI was higher at the low than at the intermediate mass (1.7 vs 2.3 ± 0.072 $g.m^{-2}.h^{-1}.LAI^{-1}$ CO_2 at 320 Wm^{-2}, $P < 0.05$) and at the higher herbage mass it was lower than the average of the other treatments (1.4 vs 2.0 ± 0.072 $g.m^{-2}.h^{-1}.LAI^{-1}CO_2$ at 320 Wm^{-2}, $P < 0.05$).

Table E3.11. Net photosynthesis per unit of LAI ($g.m^{-2}.h^{-1}LAI^{-1}$. CO_2 at 320 Wm^{-2}) in swards continuously stocked by sheep or by cattle from May to September 1980.

Treatment/Periods	Period 1	Period 2	Period 3
SL	2.1	1.6	2.7
SI	1.5	1.5	1.9
CL	2.1	2.2	2.9
CI	1.6	1.7	2.2
CH	1.1	1.5	1.8
$SE\bar{x}$			0.180

Leaf area index

Leaf area index as calculated by King *et al* (1979) for the five treatments and for the three periods is given in Table E3.12. LAI was higher in periods 1 and 2 than in period 3 (2.3 vs 2.5 vs 1.9 ± 0.18, $P < 0.05$). It was higher at the intermediate than at the low herbage mass (2.4 vs 1.5 ± 0.15, $P < 0.05$), and at the high herbage mass than the average of the other swards (2.0 vs 3.3 ± 0.15, $P < 0.05$), but it was similar on cattle- and sheep-grazed swards.

Weight per unit area of leaf

Weights per unit area for immature leaves of ryegrass and *Poa*

and for mature leaves of ryegrass, *Poa* and white clover ($\mu g\ mm^{-2}$) are given in Table E3.13. Periods were used as replicates. Weight per unit of area of the young leaf was similar for ryegrass and *Poa*. Ryegrass leaf weight per unit area was not affected by either herbage mass or animal species, but in *Poa* the low weight per unit area in the sheep paddocks at the intermediate mass and in cattle paddocks at the low mass were responsible for the interaction animal species x herbage mass being significant ($P < 0.05$). The weight per unit area of the mature leaf was affected by neither plant species nor animal species nor herbage mass.

Weight per Primary Unit

The weights of the primary units (mg $unit^{-1}$) estimated indirectly by area and weight per unit of area for ryegrass, *Poa* and white clover are given in Table E3.14. For all the three species the Period x paddocks interaction was significant ($P < 0.05$). Ryegrass tillers were heavier in period 1 and 3 than in period 2 (13.4 vs 11.4 vs 13.6 ± 0.38 mg $tiller^{-1}$) and overall they were heavier at the intermediate than at the low herbage mass (14.2 vs 9.4 ± 0.60 mg $tiller^{-1}$, $P < 0.05$). The tillers at the high herbage mass were heavier than the average of tillers on the other swards (16.9 vs 11.8 ± 0.60 mg $tillers^{-1}$, $P < 0.05$). However the weight of the tillers was the same in cattle- as in sheep-grazed swards.

Poa tillers and white clover active meristems did not show as clear a pattern as ryegrass tillers. Although *Poa* tillers became progressively lighter towards the end of the experiment (10.0 vs 9.0 vs 7.7 ± 0.27, $P < 0.05$) and clover active meristems were heavier in period 2 than periods 1 and 3 (13.7 vs 17.6 vs 13.8 ± 0.74, $P < 0.05$), the overall herbage mass x animal species was

roots and soil material were higher in extrusas collected by cattle and higher at the low than at the intermediate herbage mass.

Total stem was higher at the beginning of the experiment and then declined towards the end of the season. The composition of the extrusæ analysed under the binocular microscope from the three sub-samples bulked on a sward basis and expressed as proportion by area are given in Figure E3.15b and Table A3.19. For all the components, except total dead, the two-factor period paddock interaction was significant ($P < 0.05$). The proportion of ryegrass lamina was higher than *Poa* lamina in both cattle and sheep extrusa samples. The proportion of *Poa* was lower than 0.30 and the proportion of lamina was lower and the proportions of dead material and stem higher in cattle extrusa than in sheep extrusa samples ($P < 0.05$). The dietary overlap index (Morisita 1959; Horn, 1966) calculated from the proportions by weight (Table A3.18) are given in Table E3.19. The high coefficients indicate that dietary composition in the two species was almost identical.

Animal liveweight

The mean liveweights of the heifers, ewes and lambs maintained throughout the experimental period are depicted in Figure E3.16. Details of live-weight gains are given in Table A3.20, Appendix A3.

Heifers on the low herbage mass only maintained their initial weight while those at intermediate and high herbage mass gained 0.51 and 0.92 ± 0.072 animal^{-1}day^{-1}. Ewes on the low herbage mass lost weight while those on intermediate level maintained their initial weight. Lamb live-weight gain tended to be higher at intermediate than low herbage mass, but the differences were not

significant (0.180 vs 0.210 ± 0.020 kg animal^{-1}day^{-1}).

DISCUSSION

Statistical procedures

The experiment was unreplicated in space and the residual variance for testing between-paddock differences was calculated with the 15 degrees of freedom given by the quarters x paddocks interaction (Table D3.1). The observations were made on tillers arranged in transects distributed in quarters and these in turn were nested in paddocks. In the absence of replicates, quarters appeared to be the most homogeneous block to which each treatment was applied and it seemed more appropriate to use the quarters x paddocks interaction to estimate the residual variance rather than to use a combination of all the non-significant interactions (Cornish, 1936).

The interaction paddocks x quarters x time was used to test the differences between periods and the paddocks x periods interaction. The combined mean squares of all the interactions available was used by Bircham (1981b) in order to estimate the residual variance in similar experiments. However the high degrees of freedom resulting from such a procedure may give an under-estimation of the experimental error. In the present experiment, using all the non-significant interactions with 585 degrees of freedom as experimental error, it was possible to show significant differences ($P< 0.05$) between the net herbage production rates for cattle and sheep swards, but it was not possible to do so from the alternative model described in Table D3.1. If the assumption is made that the 585 degrees of freedom are not as realistic as the 15 shown in Table D3.1 and used in the main analyses,

the failure to detect this effect must be attributed to high variability between quarters within paddocks. The within-paddocks variance may have been affected by the progressive development of areas covered by tall vegetation which are likely to have growth relationships differing from the average of the sward. However, if quarters are accepted as a reasonable simulation of replicates, more precision in the estimation of the residual variance would have been achieved if smaller divisions than quarters had been nested within a paddock. In the present experiment the smallest subdivision of a paddock in which tiller populations were estimated was the quarter, and so no smaller hierarchy could be used in the estimate of the residual variance.

Unreplicated experiments always involve the risk of attributing between-paddock differences due to variations in natural characteristics (i.e. natural fertility or soil moisture retention) as treatment effects. The only way of separating these sources of variation is by using replicates. Replicating an experiment of this size is difficult because the amount of labour and material resources involved, and limited replication may give a low precision in the estimate of the residual variance, since few degrees of freedom are available for its estimation. However, if variability created by areas covered by tall vegetation make a substantial contribution to the residual variance, a gain in precision in the estimate may be obtained by using stratified (i.e. within kind of vegetation) rather than random sampling (Sutkhame and Sutkhame, 1970). Both replicates and stratified sampling were used in Experiment 4 and they are further discussed in page 210.

Herbage mass

The herbage mass decreased over the course of the season, though sward surface height remained relatively constant (Table E3.6). This suggests that individual tillers became progressively lighter with time. However from the marked tiller populations only *Poa* tillers became lighter as the experiment proceeded (Table E3.14). The fact that *Poa* was the dominant component in numbers may explain some of the declining trend in herbage mass when sward surface height was relatively constant. The parallel lines describing the within-period relationship between sward surface height and herbage mass (page 91) and the progressively lower intercept with time add some support to the view. Thus it appears that any given sward surface height was associated with progressively less mass as the experiment proceeded. However, although steady state in herbage mass was not fully achieved, the mean herbage masses within animal species were reasonably separated. The non-significant differences in herbage mass between animal species gives reasonable security that the effects discussed later were created by animal species and have not been confounded with herbage mass effects.

Sward surface height

Variability of the sward surface height has usually been associated with dung deposition and it has been suggested that variability declines as stocking rate increases (Spedding, 1971; Hodgson, 1974). It is believed that cattle grazing creates more variation in sward surface height than does sheep grazing, but there was no evidence that this was so in the current study. The results suggest that the variance of the sward surface

height is likely to increase with increasing herbage mass under both species grazing, although early in the season cattle appeared to create swards with high variance (see Table E3.7).

The proportion of paddocks under-grazed (Zones 1 + 2, Table E3.8) are in the range of proportions quoted for beef and dairy cattle grazing in a range of conditions (see Marsh and Campling,1970), but there is no equivalent published information for grazing sheep. The area refused by cattle grazing at intermediate mass was lower than expected. This may have been the result of the heights chosen to establish the limits between zones in that particular treatment, rather than to a true low proportion of the area refused. Cattle and sheep appeared to leave equivalent proportion of areas undergrazed in the vicinity of their own dung.

Sward botanical composition

The proportion of lamina in the sward increased as herbage mass increased, as would be expected from reported experience (Bircham, 1981b), and the proportion of ryegrass lamina increased relative to that of *Poa* lamina. This may be explained by the fact that young ryegrass laminae were more abundant in the upper horizons of the canopy (Figure E3.3, 3.4, 3.5 and E3.6a) and they would have had higher chance of being reduced by defoliation as the herbage mass decreased (Barthram, 1980). Cattle- and sheep-grazed swards were similar in botanical composition, sward structure and geometry (see page 94). However some changes in botanical composition may be expected since the losses of tillers to uprooting may be different for different animal species (Monteath *et al*, 1977). In the present experiment the net rate of tiller

appearance for ryegrass tended to be lower than for *Poa* (Figure E3.10) but this was not reflected in changes in botanical composition during the experimental period. However, ryegrass tillers as a proportion of the total population fell from 0.34 in September to 0.20 in the following April in cattle-grazed swards, while in sheep-grazed swards the changes were negligible (0.41 to 0.37). Thus it appears that differences in botanical composition between swards grazed by different animal species could occur in the long term.

The proportion of total dead tissue and its components, dead tissue attached and detached , were not as similar between treatments as the proportion of leaf lamina, but they converged to similar ratios by the end of the season (Table E3.9).

Tiller population dynamics

The main components of the sward population were *Poa* and ryegrass tillers; white clover was a minor component distributed in irregular and small areas in all paddocks.

The rates of tiller appearance and disappearance were within the range found in vegetative swards of timothy, meadow fescue and cocksfoot (Langer *et al*, 1964; Bean, 1964). However, Tallowin (1981) reported lower rates on ryegrass swards grazed by cattle at similar sward surface height. The turnover of tillers was high in June and July and then declined towards the end of the season. When rate of appearance within a paddock was high so was the rate of tiller disappearance (Figure E3.10) and the seasonal variation in net change was not great. This is in line with observations in cut swards (Langer *et al*, 1964). However,

there were some exceptions to this generalisation. For example, in the short sward grazed by sheep the net appearance rate for ryegrass and *Poa* tillers ranged from 4.0 to -0.33 and 4.0 to 1.17 tillers.100 tillers^{-1}.day^{-1}respectively. However, while the low value in ryegrass was due to relatively high rate of disappearance, the low rate in *Poa* was due to a relatively low rate of appearance.

The lower tiller numbers in cattle-grazed swards may be explained by higher rates of tiller loss under cattle grazing, and are in line with other evidence reported in the literature (Mitchell and Glenday, 1958; Boswell and Crawford, 1978; Briseno de La Hoz and Wilman, 1981). The high rate of tiller disappearance in cattle-grazed swards was presumably due to higher tiller uprooting. Although the causes of tiller disappearance were not determined in this experiment it has been observed that grazing cattle pull out more tillers than grazing sheep (Monteath *et al*, 1977; Boswell and Crawford, 1978).

The higher tiller density at the low herbage mass, on the other hand, was due to a higher rate of tiller appearance and this may be expected since in short swards more light would have reached the base of the tillers, resulting in the stimulation of more tiller buds (Mitchell and Coles, 1955). This is in general agreement with the evidence that severe grazing encourages the development of a more dense sward than does lax grazing (Brougham, 1959; Wade, 1979; Bircham and Hodgson, 1981; Tallowin, 1981; Grant *et al*, 1981a). However the differences in tiller density in cattle-grazed swards were not significant, presumably because the higher rate of tiller appearance at the low herbage mass was compensated by a higher rate of tiller disappearance, so

the net rate of tiller appearance was not greatly affected.

The difference in tiller numbers which was established between swards grazed by cattle and by sheep over the course of the season was still maintained in the following spring (Figure E3.9). This suggests that if the same trends in tiller turnover are repeated season after season, cattle-grazed swards would continue thinning to extinction. However, from long term experiments it appears that cattle-grazed swards stabilize at lower tiller densities than sheep-grazed swards, and that densities may be reversed within a grazing season by switching the animal species grazing on the sward (Monteath *et al*, 1977; Boswell and Crawford, 1978).

The reversed pattern in total tiller populations between low and intermediate herbage mass over the winter suggests that crowded populations of small tillers are more sensitive to winter stress than sparser populations of bigger tillers. Alternatively, if there is a peak of appearance in February-March as described by Langer *et al* (1964), the more open sward may have received more light in the base of the tillers and so more buds may have developed (Mitchell and Coles, 1955; Langer, 1979). Perhaps the more interesting aspect of the tiller population after winter was the fall in ryegrass tillers in cattle plots from 0.34 to 0.20 of the total population compared with the constant population in sheep-grazed swards (0.41 to 0.37). Progressive reduction in the ryegrass component has been attributed to a high loss to uprooting due to the characteristic pulling action of grazing cattle (Monteath *et al*, 1977). In the present experiment, however, the further reduction in ryegrass tillers during the winter cannot be explained by such

(Davidson and Robson, 1981). However, the photosynthetic capacity of the youngest leaf is only one of the factors which control the photosynthetic rate of the whole plant, and other important factors such as leaf area per tiller or active meristem, and geometry of the leaf canopy, which influence light interception will also influence the rate of photosynthesis. The rate of lamina senescence per primary unit was highest in clover followed by ryegrass and then *Poa*, but the number of leaves showing senescence was highest in *Poa* followed by ryegrass and then clover (1.0 vs 0.8 vs 0.5 ± 0.02 leaves.primary unit^{-1}, $P < 0.05$). The relative lamina senescence rate was highest in *Poa* followed by clover and ryegrass (0.016 vs 0.014 vs 0.013 ± 0.0006 mg mg^{-1}.day^{-1}, $P < 0.05$). The higher rate of lamina senescence in *Poa* may be explained by its relative location within the canopy. Assuming that the same distribution for the youngest leaves was maintained for the expanded leaves (Bircham, 1981b) and that clover leaves reach the top of the canopy before full expansion (Davidson and Robson, 1981), most of the *Poa* expanded leaves may be in the lower horizon of the canopy. As the grazing animal appears to graze by superimposed horizons (Hodgson, 1982) the probability of a *Poa* lamina being defoliated was lower compared with the probability of defoliation for the other two species. Taken together, all these observations suggest that the ageing *Poa* tissue within the canopy which was not defoliated must have followed the senescence pathway (Bircham and Hodgson, 1981). As a matter of fact, *Poa* lamina was found in a very low proportion of the diets of cattle and sheep (Figure E3.15b) compared with ryegrass lamina proportion, despite being in similar proportions in the sward (Table E3.9).

The growth rate per primary unit in ryegrass and *Poa* tended to increase with herbage mass, in parallel with the leaf area per tiller but, since senescence rate tended to follow a similar pattern, between-mass differences in net production were very small (Figure E3.11). The high growth and senescence rate for ryegrass in the sheep-grazed sward at the intermediate mass in period 2 is difficult to explain in biological terms. However, as areas of tall and short vegetation were not uniform between swards, more tillers within a tall area may have been allocated by chance to this paddock in this particular period.

Clover active meristems, on the other hand, did not show a clear pattern across masses but, as clover meristems were not distributed at random, the growth per individual may have been affected by particular characteristics other than herbage mass or sward surface height. The characteristic patchiness in the clover distribution may deserve particular attention when extrapolations from the individual to the population have to be made. Animal species did not affect any of the rates in grasses, but clover growth rate was higher in cattle-grazed than sheep-grazed swards (Figure E3.11c) and, although the rate of clover senescence was higher in cattle-grazed swards as well, net growth rate was still higher under cattle grazing. The low rate of net growth per active meristem in sheep-grazed swards suggests a small size for the clover primary unit under grazing sheep. This reduction in size has been suggested as a mechanism of adaptation of the clover plant to a preferential grazing by sheep (Briseno de La Hoz and Wilman, 1981). But in this experiment the size of the marked active meristem was not affected by animal species (see Table E3.14).

Plant Species Performance per Unit Area

The growth per unit area is in part regulated by the growth rate of the individual plant unit, but certainly it is strongly related to number of individuals. Competition, stress, and disturbance have been suggested as determinants of vegetation, and relative growth rate and size of the canopy as plant attributes giving competitive advantages (Grime, 1974). These two attributes give in theory competitive advantages to ryegrass over *Poa* (see page 139) and under low disturbance or lax defoliation *Poa* may be suppressed by ryegrass because both species overlap niches (Harper, 1970). However, grazing, by reducing ryegrass leaf area, released *Poa* from suppression with a consequent change in the between-species relationships. In this experiment the average proportions of *Poa* and ryegrass in the high and low herbage mass swards grazed by cattle were 0.4-0.51 and 0.59-0.39 respectively, and bigger differences have been quoted in sheep grazed swards (Bircham, 1981b). Ryegrass populations at the low herbage mass and in both low and intermediate masses grazed by cattle fell during the winter while *Poa* remained constant. This kind of management producing high disturbance in the ryegrass population may give the opportunity to a quick colonizer to fill the niche normally occupied by ryegrass (Grime, 1974; Wells, 1974).

Both ryegrass and *Poa* appeared to have similar relationships between the individual and the population, and similar responses to management as well. In the sheep-grazed sward at the low herbage mass there were many small tillers growing at a low rate, while at the intermediate herbage mass there were fewer tillers growing at relatively high rate. This reciprocal association between

numbers and individual performance was less apparent in cattle-grazed swards since tiller densities were not affected by herbage mass. Similar relationships between densities and weight of the survivors have been described for a range of woody and herbaceous species growing undisturbed (Yoda *et al*, 1963; White and Harper, 1970; Kays and Harper, 1974) and for ryegrass-dominant swards grazed by sheep (Hodgson *et al*, 1981). The relationship seems to hold for individual plant growth and even for organs of the plant, at least in herbs allowed to grow undisturbed (White and Harper, 1970).

Taken together all these observations suggest that, when disturbance on the plant population is not severe, growth of organs and individuals may be density regulated. When the sward surface is fixed by management decisions, the number of tillers develops in equilibrium with an average individual size. But if other external factors (e.g. uprooting) operate, self-regulatory properties are lost. Hodgson *et al*, (1981) showed that at very low herbage mass, when uprooting was presumably high, the stability of the relationship between density and weight of the survivors was broken. In this experiment tiller density was lower in cattle- than in sheep-grazed swards, but the mean weight of the marked tillers was not affected by animal species. Individual tiller growth was higher at the high herbage mass for both animal species (Figure E3.11) and animal species grazing did not affect growth rate per tiller. Following White and Harper (1970), under undisturbed growth the less dense sward should have grown at a higher rate per individual. However, as density was reduced by cattle grazing and height was fixed by management, the individual

tiller could not compensate by growing faster since there was not much flexibility to increase in lamina and sheath breadth. This observation suggests that the shorter the sward grazed by cattle the lower the growth rate per unit area may be expected to be.

Combined Species Performance

The seasonal pattern of growth rate is in good agreement with general patterns described elsewhere from cutting experiments (Anslow and Green, 1967), but the absolute growth rate per unit area was higher in the current experiment. However, the rates lie within the range reported by several authors under grazing conditions (Morris, 1970; Bircham, 1981b; S.A. Grant, personal communication). The rates in June-July were lower than in August and September, presumably because of the low number of tillers or because of severe drought during May and June (50 mm less precipitation than the 50 year May and June average) or both.

Overall growth rate increased with herbage mass in line with other published evidence (Bircham and Hodgson, 1981). However, within cattle swards growth rate seemed to reach a plateau between the intermediate and the high herbage mass. This may be largely explained by the lower photosynthetic capacity of the young leaves developed in the presumably poor light environment on the higher LAI swards (Woledge, 1978). Sheep-grazed swards grew faster than cattle-grazed swards and this may be explained in terms of differences in tiller number as discussed before. The growth rate per primary active clover meristem, was higher in cattle than in sheep-grazed swards (Figure E3.11), but because of the low number of individuals, the contribution of clover to the total growth rate was negligible (Figure E3.12). This result suggests that if

the higher growth per active meristem is not counterbalanced by a higher uprooting of clover meristems by cattle grazing (Boswell and Crawford, 1978), a higher clover population than that observed in this experiment, may offset the effects of animal species on the grass tiller populations. However, the characteristic non-random distribution of white clover observed in this experiment and others (Bircham, 1981b) may make difficult the extrapolation of the clover contribution to the rates on the whole paddock.

Net canopy photosynthesis per unit of LAI was not significantly affected by animal species (Table E3.11) and this suggests that leaf photosynthetic potential and canopy structure was similar in the cattle- and sheep-grazed swards.

Rate of Lamina Senescence

The rates of lamina senescence in this experiment ranged from 15 to 43 kg.dm.ha^{-1}.day^{-1}, and similar values have been reported by other workers (Tainton, 1974; Wade, 1979; Bircham, 1981b). The rate of senescence increased as herbage mass increased, an observation largely explained by the fact that both the size of the leaf and the opportunities for senescing before being harvested increase as herbage mass increases. The higher lamina senescence rate observed in sheep-grazed swards appeared to be largely due to a density effect. Since sheep swards had higher density, the ageing tissue may have received less light than it would in cattle swards and so more tissue may have senesced in the same period of time (Brougham, 1958; Harper, 1977; Leopold, 1980).

Net Herbage Production

Net production has been described as insensitive to herbage mass over a range of conditions (Hodgson and Wade, 1978; Bircham and Hodgson, 1981). Bircham and Hodgson (1981) reported that net production was constant over a range of herbage masses between 1000 and 1700 $kg.ha^{-1}$ in swards grazed by sheep in the same environment. In the present experiment net production was apparently still increasing at the intermediate herbage mass only when grazed by sheep. These results can be explained in terms of self-regulatory mechanisms between the individual and the population. The swards described by Bircham and Hodgson (1981) were more dense than the swards in the current experiment and in this condition higher senescence balanced higher growth rate at the tiller level and net growth of the population remained constant. This may be interpreted as if the plant population over this range of mass reached the capacity for the environment and the net growth rate reached an equilibrium with mineral resources and space (Odum, 1971). In the present experiment the population in the sheep-grazed swards were 0.75 of the population reported by Bircham and Hodgson (1981) and the "carrying capacity" of the environment was probably not reached. In these circumstances, an increase in net growth rate may be expected until a higher degree of overcrowding is reached. However, the swards grazed by cattle reached a plateau between intermediate and high herbage mass, and tiller populations were lower than in sheep-grazed swards. In these swards, the lower photosynthetic capacity of the leaves as herbage mass increased (Table E3.11) may have restricted the potential population capacity for exploiting the environment. This view is supported by the

fact that growth and senescence rate did not differ significantly between intermediate and high herbage mass (Figure E3.13 and Table A3.17, Appendix A3).

The effect of animal species on the rate of net production was not significant ($P < 0.05$) although the differences were 1.7 times those for ryegrass alone (see Figure E3.12 and E3.13). However the separation between treatment means for ryegrass was done with a lower standard error because more degrees of freedom were available since three plant species were involved in the analysis (see page 89). Thus, it is possible that the non-significant effect of animal species on net production was due to limitations of the analysis and that the treatment effects were real. As a matter of fact if a lower residual variance had been used to test the differences, such as the paddocks x quarters x transect interaction with 20 degrees of freedom (Table D3.1) the differences would have been significant ($P < 0.05$).

In long-term experiments, differences in net production between cattle- and sheep-grazed swards have developed after the first year (Monteath *et al*, 1977), although differences in the first year have already been reported (Boswell, 1978). In the current experiment the absence of differences in the rate of herbage production may have been due to the low sensitivity of the model used in the analysis rather than because the effect developed slowly over time.

Net production as estimated in this experiment is the accumulation of green herbage that would have occurred had it not been consumed, and no other causes of tissue disappearance

than senescence have been considered. Tissue flow on uprooted tillers was not included in the calculations in this experiment, though this may be an important source of tissue losses, particularly in cattle-grazed swards.

Herbage Consumption per Unit Area

Total herbage consumption per hectare did not match net production (Tables E3.17 and A3.17) so equation R.2 (page 10) was not satisfied. The differences between total herbage consumption and net production rates were sometimes positive and sometimes negative and may be in part due to errors in estimating the rates of herbage growth and/or intake over short periods of time. It is surprising that this imbalance between net production and total harvest occurred under apparently constant sward surface height and under reasonably constant (at least in periods 2 and 3) herbage mass. Bircham (1981b) reported practical difficulties in maintaining the theoretical assumption that NHA = 0. The herbage accumulation calculated by difference between herbage mass before and after each detailed measurement period was not related to the accumulated balance between net herbage production and harvest rates, presumably because relatively few samples were involved in individual estimates of herbage mass. When net herbage accumulation was calculated from differences in average herbage mass between two periods a better agreement with the balance of the rates within period was found (Table D3.2).

For Period 1 the rate of herbage consumption was higher than the rate of net production, i.e. rate of net accumulation was negative. This may have been a consequence of over-stocking aimed

to adjust sward surface height to the target values. As a matter of fact there was a good agreement between the changes in herbage mass between periods 1 and 2, and estimates of the rate of net herbage accumulation (i.e. net production rate minus herbage consumption rate) (Table D3.2). However, the rate of intake per animal declined with time (Table E3.16) and so did the stocking rate and this was reflected in a decline in total herbage consumption in periods 2 and 3 (Table E3.17). In Period 2 the total herbage consumption rate was equal to net production rate at the low herbage mass and this was reflected in the negligible change in herbage mass detected between periods 2 and 3 (Table D3.2). The rate of herbage consumption was lower than net production rate at intermediate herbage mass and at the high herbage mass grazed by cattle, but these differences were not reflected in equivalent changes in herbage mass between periods 2 and 3 (Table D3.2). In period 3, however, the sheep-grazed swards were near the steady state, while cattle-grazed swards were harvested at a higher rate than the rate of net production so net accumulation rate was negative. Although from these observations steady state in herbage mass may be questioned, the changes in comparable cattle- and sheep-grazed swards may be regarded as equivalent.

Animal Measurements

Herbage intake

The organic matter intakes (Table E3.16a, b) were lower than values reported for ewes and lambs in comparable sward studies by Bircham (1981b) and rates of intake for calves and lambs by Jamieson and Hodgson (1979). These low intake rates are difficult to explain in biological terms, although the faecal ash content tended

to be high on all treatments (0.3 to 0.5) which would suggest that ingestion of soil was high. However the rate of intake in metabolizable energy calculated from the measured rates are *c a.* 0.8 of those recommended in standard tables for similar live-weight gains in cattle and for lactating ewes (ARC, 1980). Checks on analytical procedures revealed no obvious reasons for under-estimation of intake, and the differences between the estimates in this experiment and those reported by Jamieson and Hodgson (1979) and Bircham (1981b), may be partially explained by differences in the phsiological status of the animals and by differences in sward characteristics.

The rate of intake decreased with time in both sheep and cattle, presumably as a consequence of the decline in herbage mass with time, but the drop was higher at the intermediate than at the low herbage mass. Cattle grazing at the high herbage mass maintained a constant rate of intake over time. Similar trends in time have been reported by Bircham (1981b) for grazing sheep and, as in the present experiment, the interaction treatment x period was not significant for the lamb's rate of intake. The drop in the rate of intake per unit of live weight from intermediate to low mass was higher in cattle than in sheep (Table E3.16b) and this may reflect the anatomical difficulties of cattle in harvesting short vegetation (Leigh, 1974).

Grazing Time and Diet Quality

Grazing time was not affected by changes in herbage mass either in cattle or sheep (Table E3.18). This may be expected since variation in intake per bite appears to be greater than variations in either biting rate of grazing time in both cattle and

sheep (Bircham, 1981b; Hodgson, 1982).

Sheep spent more time grazing than cattle and this result is in line with those reported by Jamieson and Hodgson (1979) and by Forbes (1982). The longer time spent by the sheep grazing reflected differences in selection of the diet consumed (Figure E3.15). Sheep selected a diet richer in lamina which had less stem, dead tissue and roots than the diet selected by cattle. Similar results have been reported for cattle and sheep grazing in the same paddock (Dudzinski and Arnold, 1973; Hodgson and Grant, 1981; Forbes, 1982). In the present experiment the animal species grazed in separate paddocks and, although the sward was originally the same, it can be argued that grazing effects may have changed the original balance between plant species, and that differences in diet composition then may be explained by differences in the swards. However, botanical composition at comparable herbage mass was uniform and this uniformity increased towards the end of the season (Table E3.9). Between-treatment differences in the botanical composition of both the sward and the extrusae were higher at the beginning than at the end of the season (Figures E3.2 to E3.5 and Table E3.8). These results suggest that when the opportunities for selection were high (e.g. periods 1 and 2) sheep were able to harvest a diet richer in lamina and lower in dead tissue, stem and roots than cattle. However when diversity in the sward was reduced (e.g. period 3) the differences in diet selection disappeared. The high dietary overlaps (Table E3.19) indicated that the two species did not have different nutritional niches and so they would not be expected

to use vegetation in a complementary manner when grazed together. On the other hand, the higher stem proportion in the diet of both species in Period 1, compared with the other two periods, suggests that both cattle and sheep tend to graze by superimposed horizons rather than in a selective fashion (Hodgson, 1982). The lower proportion of *Poa* lamina (Figure E3.15b) in both cattle and sheep diets may give some support to this view. The youngest *Poa* lamina was overtopped by the youngest ryegrass lamina (Figures E3.6a and b) and this reduced the chances for *Poa* being defoliated. The lower frequency of defoliation for *Poa* tillers in both cattle- and sheep-grazed swards supports the above argument.

The differences in botanical composition were reflected in differences in the digestibility of the diet (Table E3.15); i.e. the differences in digestibility of extrusae were significant only at the beginning of the experiment. The quality of the diet selected by sheep has normally been found to be higher than the quality of the diet selected by cattle (Dudzinski and Arnold, 1973; Langlands and Sanson, 1976; Jamieson and Hodgson, 1979). However, as in the case of diet botanical composition, the differences disappeared when diversity in the sward was reduced as the herbage mass declined. The observations on diet composition and quality support the views by Hodgson and Forbes (1980) that differences in the diet selected by the two species are likely to be of little agricultural significance in intensively grazed swards.

Animal Production

Cattle and sheep appeared to show similar patterns of intake and diet selection to variation in herbage mass and sward surface height. However, the low performance in cattle grazing at the low

herbage mass suggests that levels of herbage mass satisfactory for sustaining acceptable lamb growth rates may not be adequate to sustain acceptable growth rate in cattle. But the acceptable growth rate in lambs was maintained at the expense of losses in the live weight of their dams. The high individual performance in cattle grazing at the high herbage mass was associated with the highest rate of herbage senescence. This result suggests that high performance per individual is subsidised by high losses of energy through the senescence pathway.

Animal production per unit of area in the cattle swards was similar at the intermediate and high herbage mass (700 vs 750 $kg.ha^{-1}$, in 136 grazing days) but it was low at the low herbage mass (130$kg.ha^{-1}$ in 136 grazing days). In the sheep-grazed swards lamb meat production was 560 and 490 $kg.ha^{-1}$ in 105 grazing days for low and intermediate herbage mass respectively. These estimations of animal production are only illustrative, and since they were calculated from a put-and-take system their relevance to the farm practice may be questioned (Morley and Spedding, 1968; Morley, 1978). Comparison of animal production per area between cattle and sheep is further complicated by difficulties in finding equivalences between wool and meat production. However cattle production was clearly much more sensitive to changing sward conditions than was sheep production, in line with the observed intake responses.

The stocking rates used to maintain sward surface height constant (Figure E3.15) provide estimates of equivalence in animals as harvesters. Equivalents were approximately 2 ewes + lambs to 1 heifer. However, as animal performance was very different on the shorter herbage mass, the equivalents as harvesters were not a good

indicator of the equivalents for production. Weaned lambs might react in similar fashion to young cattle to changes in herbage mass. Nevertheless this result suggests that difficulties in equating animals in experiments where animal production is the main interest (Connolly and Nolan, 1976) may be overcome by applying some degree of control on the sward parameters such as herbage mass of sward surface height.

Mixed Stocked Systems

One of the main reasons for comparing sheep- and cattle-grazing systems is to improve the understanding of their structure and function with the ultimate objective of discovering the likely agricultural advantages in grazing the species single or in combination.

Complementary theories have been suggested to justify the higher animal performance in mix-stocked systems (Nolan and Connolly, 1977; Nolan, 1977; Nolan, 1980; Connolly, 1980). However from the analysis of single species systems in this experiment, complementary patterns are not clearly shown. These results support the view by Hodgson and Forbes (1980) that most of the differences between species, if operative in mix-stocked systems, seem to operate in one direction rather than in a complementary fashion. In other words, mixed stocked systems are likely to be more similar to the animal species that is in the highest proportion in the mix. For example, if tiller number is reduced because cattle pull them out and in turn tiller population affects the rate of net herbage production, the higher the proportion of cattle the more similar will be net herbage production to that in swards grazed by cattle alone. However, this does not necessarily mean that net herbage production will be linearly related to the proportion of animal species grazing,

since the effect of a low proportion of cattle in reducing tiller number may be no greater than the effect of sheep grazing alone. These possibilities lead to the suggestion that mixed-stocked systems are likely to have higher net herbage production than cattle-stocked systems, but it is unlikely that net herbage production will be higher than in sheep-stocked systems. On the other hand, the advantages of sheep in being better able to maintain intake and possibly select a more digestible diet may give competitive advantages to sheep in mixed grazing systems, so that any increased sheep output will be to the detriment of cattle output.

Grazing efficiency under combined species grazing may be increased if site selection (Milne *et al*, 1979) and bite selection are complementary. The opportunities for choosing a particular site under intensive management are likely to be associated with the ungrazed vegetation in the vicinity of the dung patches (Hodgson, 1982). In this experiment the responses of the two species to their own dung were very similar, and the proportionate areas of herbage left behind under-utilised were similar for cattle and sheep (Table E3.7). Also, bite selection, as illustrated by the botanical composition of the diet, appeared not to be greatly different between species. The fact that the marked units were, overall, more frequently defoliated by sheep than by cattle may be an indication that sheep remove less tissue at a defoliation, but graze individual tillers more frequently than cattle. This characteristic may be interpreted in terms of greater selectivity by sheep than by cattle, but, because the vegetation was not diverse enough, botanical composition of the diets was not different between species. These hypotheses were tested in a second field experiment and they are further discussed in Experiment 4.

CHAPTER 5

EXPERIMENT 4

INTRODUCTION

Experiment 3 was conducted to study tissue flow in cattle and sheep grazing systems under comparable conditions. Tiller population densities, and growth and net production rates became progressively higher in sheep- than in cattle-grazed swards and the differences were significant by the end of the season. The lower tiller population in cattle-grazed swards appeared to be the result of higher tiller disappearance rates under cattle grazing.

It was postulated that under mixed animal species grazing tiller population densities, herbage growth and net production rates may be similar in swards grazed by a combination of sheep and cattle and in swards grazed by sheep alone.

This experiment was conducted to confirm the results from Experiment 3 and to test the above hypothesis. The same techniques as in Experiment 3 were used to study the tissue fluxes under grazing by sheep or cattle alone and under a mix of both species under comparable sward conditions.

General

The experiment was conducted during the summer of 1981 on the Reservoir field at the Hill Farming Research Organisation's Hartwood Research Station, situated close to Shotts on the western edge of Strathclyde Region, Scotland (230 m altitude; $3^{o}50.4'$ long, N, $55^{o}48.8'$ lat. N - 1042 mm rainfall $year^{-1}$ average of 60 years).

The field (Plate E4.1) was cultivated and sown with *Lolium perenne*, L. cv. S23 and *Trifolium repens*, L. cv. *Huia* in the summer 1980. A compound fertiliser (30 kg ha^{-1} N_2; 22 kg ha^{-1} P_2O_5; 22 kg ha^{-1} K_2O) and triple superphosphate (28 kg ha^{-1} N_2; 73 kg ha^{-1} P_2O_5) were applied at sowing.

Sward Management and Experimental Design

The field was grazed by sheep from April to end of May 1981 when it was closed to grazing and a silage cut was taken in the last week of June. A compound fertiliser (N = 30 kg ha^{-1}; P_2O_5 = 22 kg ha^{-1}; K_2O = 22 kg ha^{-1}) was applied at the beginning of April and again (N = 30 kg ha^{-1}; P_2O_5 = 22 kg ha^{-1}; K_2O = 22 kg ha^{-1}) the second fortnight in August.

In the last week in July twelve paddocks were established and six treatments were allocated with two replicates (Figure E4.1). The treatments were the result of a combination of two levels of predicted herbage mass, 1300 and 1700 kg ha^{-1}, monitored by sward surface height (3.0 cm and 4,5 cm) and three different populations of grazing animals. The animal populations were cattle and sheep grazing alone and a combination of both species. The equivalents between species were determined from Experiment 3 as 1 yearling cattle unit of intake being equivalent to 3 wether units of intake, and both species were combined in a 1:1 proportion on intake basis. The greater sward surface height compared with Experiment 3 was decided upon in order to provide more realistic herbage mass levels for cattle grazing (see page 153). The procedures used in Experiment 3 to establish the mass required and for maintaining swards in steady state were also used here.

Animals

Mature Blackface wethers and yearling male Friesian cattle were weighed non-fasted and allocated to treatments at initially similar average live weights within animal species. Four heifers fistulated at the oesophagus (two prepared in April and two used the year before in Experiment 3), and four fistulated ewes which

were used in Experiment 3 were grazed with the non-fistulated animals. All animals were drenched with the proprietary anthelmintic.

Experimental Measurements

The techniques used in Experiment 3 to measure herbage mass, sward surface height, species population density, tissue turnover and the associated measurements for leaf area and weight conversions, faecal output, diet botanical composition and digestibility were used in this experiment also. There was a single detailed measurement period during the first fortnight in September. From observations made in Experiment 3, it was decided to study the fluxes of plant tissue in two different sectors in the sward, the "tall" areas mainly associated with dung deposition and the "short" areas associated with more frequent grazing. On the basis of the sward profile estimates in Experiment 3, it was decided to allocate 20% of the observations to the "tall" areas and 80% to the "short" areas.

Herbage mass was estimated by eight 1.22 m x 0.15 m quadrat frames per replicate cut every fortnight from the beginning until the end of the experiment.

Tiller and stolon density was estimated from 0.05 m x 0.10 m quadrats on twenty turves per replicate (40 per treatment) taken from the field to the laboratory in the first week in September and again in the first week in October. Sixteen turves were dug from the short vegetation areas and four from the tall vegetation areas, and tillers for ryegrass and *Poa* and active meristems for clover were counted as in Experiment 3. Two extra random samplings were done, one before the treatments were allocated (3rd week in June) and the other at the beginning of the following season (first

week in May). In the first sampling no differentiation was made between grass species.

Tiller turnover rates were estimated in one of the replicates. Two techniques were used and rates of appearance, disappearance and net change in the population of perennial ryegrass tillers were measured.

Technique a.

During the first three weeks in August four cohorts of *c a.* twenty tillers per treatment were chosen at random and the pseudostem of every tiller was painted with orange oil paint, using a syringe. The cohort was then surrounded with a plastic coated wire ring anchored with 2 flat-head nails 60 mm long. Each cohort was removed seven days later and painted and unpainted tillers were counted and the increments and decrements were calculated by difference. Every week a fresh cohort was marked.

Technique b.

In the first week in August twenty tillers per treatment were selected at random and marked in four transects of five tillers as in Experiment 3 (see technique used to select tillers for tissue turnover estimations). Each tiller was observed once a week during the next eight weeks and records were made of the presence or absence of the original tiller and of any new daughter tillers. Each new tiller was marked with a ring of different colour one week after being detected, and observed until the end of the experiment (1st of October).

From both techniques gross appearance and disappearance rates were calculated as described in Experiment 3. Both techniques were used during a comparative period lasting 21 days, and technique

b was continued for a further 5 week period. In addition, rates of tiller turnover were calculated over 14 days from tillers marked for tissue turnover.

The structure and the botanical composition of the swards was determined using an inclined(32.5^{o}) point quadrat (Warren-Wilson, 1963; Grant, 1981). Fifteen randomly selected sampling sites were used on each plot but sampling was continued until 100 contacts per plot had been recorded. All contacts were recorded as the needle passed through the sward. Each contact was identified in terms of species, morphological unit, and whether live or dead. The data from all contacts were summed within 2 cm strata and the proportion of the following components was calculated for each species:total lamina, total stem, total dead and total green (lamina plus stem).

In order to describe the variation in sward surface profile, two transects 25 m long were permanently marked in each plot as in Experiment 3. The undisturbed surface height of the sward canopy was recorded at 0.2 m intervals along each transect on three occasions, in the second and in the last week in July and in the last week in August. The canopy height was estimated using a rod with a perspex slide (Bircham, 1981b).

In each plot three transects of four tillers per species were allocated at random in the areas covered by short vegetation and one transect per plant species was allocated in the areas covered by tall vegetation. Thus 576 units (twelve tillers per plant species in the short and four tillers per plant species in the tall areas per treatment per replicate) were marked and measured as described in Experiment 3. The proportions of tall and

short areas of vegetation in each paddock were estimated by a modification of the step technique (Cockayne, 1926), in which an observer moving at random within a paddock recorded, at each step, if the toe of his boot touched a tall or short area of vegetation. A tall area was defined as the area covered by leniently or undefoliated vegetation whether or not it was associated with a dung pat. A short area was defined as the area covered by the vegetation of predominant height in the paddock. In this way a minimum of 1000 observations were recorded per plot and the proportion of points recorded as tall was calculated.

The proportions of areas covered by tall and short vegetation were used to define the relative size of the strata and as a basis for calculating weighted mean values (Sukhatme and Sukhatme, 1970). The 12 estimates for the short areas (3 transects x 4 tillers) were averaged over tillers and estimates weighted for the selective proportion of each area were summed. In this way four weighted primary unit estimates were nested in each paddock for the analysis of variance. Standard ANOVA techniques available in GENSTAT version 4.03 as implemented by Edinburgh Regional Computing Centre were used (Table E4.1). The gain in precision from stratified sampling compared to random sampling was calculated as suggested by Sukhatme and Sukhatme (1970) for the following parameters: herbage mass, total and per species densities, and growth, senescence and net growth per primary unit, per species and total sward rates.

RESULTS

Introduction

Mean treatment effects are presented in tables or block diagrams for the short and tall areas and for the whole plot weighted

by proportions of short and tall areas. When values are presented as diagrams the means and standard errors are given in a table in Appendix 4.

The actual weighted mean herbage masses 1600 and 1900 kg ha^{-1} OM will henceforth be used to describe the herbage mass levels.

Proportion of the area covered by tall vegetation

The proportion of the plot area of each treatment covered by tall vegetation is given in Table E4.2. The proportion covered by tall vegetation was higher at the 1900 mass than at the 1600 mass (0.40 vs 0.26 ± 0.014, $P < 0.05$) and it was higher in sheep- than in mix- and cattle-stocked swards (0.39 vs 0.33 vs 0.28 ± 0.010). The interaction herbage mass x animal species was not significant.

Table E4.2. Proportion of the area covered by tall vegetation.

Herbage Mass/Animal Species	Cattle	Sheep	Sheep + Cattle	$\bar{x}$	$SE\bar{x}$
1600	0.24	0.29	0.26	0.26	
1900	0.32	0.49	0.40	0.40	0.014
$\bar{x}$	0.28	0.39	0.33		
$SE\bar{x}$			0.018		

Herbage Mass and Sward Surface Height

The estimation of herbage mass for the tall and short areas and weighted for the proportion of the corresponding areas to give an average per paddock, and of sward surface height taken at random, are given in Table E4.3.

Herbage mass was not affected by treatment in tall vegetation

Table E4.4. Mean variances of the sward surface height (cm^{-2}) in swards grazed by cattle and sheep alone and in combination.

		Animal species		
Period	HM	Cattle	Sheep	Cattle + Sheep
beg. July	1600	34.1	29.8	36.8
	1900	31.8	36.2	24.1
end July	1600	32.8	19.0	27.6
	1900	37.1	32.4	35.7
August	1600	50.5	12.0	17.1
	1900	56.8	38.8	49.3
$SE\bar{x}$				0.71

but in the short vegetation areas it was lower at the 1600 than at the 1900 mass (1400 vs 1700 ± 60 kg dm ha^{-1}, $P < 0.05$) but it was not affected by animal species. The weighted average was lower at the 1600 than at 1900 mass (1600 vs 1900 ± 90 kg dm ha^{-1}, $P < 0.05$) and again it was not affected by animal species.

Sward surface height was not affected by animal species, and the differences between herbage mass were within the expected range (3.0 vs 4.4 ± 0.13 cm, $P < 0.05$).

Variation in Sward Surface Height

As in Experiment 3, a linear model was fitted to the within-plots variances of the sward surface height measurements recorded along the fixed 25 m long transects. As the residual variance was too great to allow the deviance to be tested against a X^2 (Baker and Nelder, 1978) the treatment effects on the variances were tested against F.

The mean variances per treatment for the three periods are given in Table E4.4. The three-factor animal species x herbage mass x period interaction was significant ($P < 0.05$) but the two-factor herbage mass x animal species interaction was not. The variance of the sward surface height was higher on the 1600 than on the 1900 sward during the first observation (33.6 vs 30.7 ± 0.41 cm^2, $P < 0.05$) but the variance was reversed by the end of July and the same relationship was observed by the end of August (26.5 vs 35.1 and 26.5 vs 48.3 ± 0.41 cm^{-2} for end of July and end of August respectively, $P < 0.05$).

The animal effect developed gradually. At the beginning of July the variance in the mix-stocked swards was lower than in cattle- or sheep-stocked swards (30.5 vs 33.0 vs 33.0 ± 0.50 cm^{-2}, $P < 0.05$), but the highest variance was observed in cattle- followed by mix- and sheep-stocked swards in July (35.0 vs 31.7

vs 25.7 ± 0.5 cm^{-2}, $P < 0.05$) and in August (53.6 vs 33.2 vs 25.4 cm^{-2}, $P < 0.05$).

Sward Botanical Composition

The proportions of live ryegrass, *Poa* and white clover were not affected by either herbage mass or animal species either in the area covered by tall or short vegetation or in the whole area weighted for the proportion of the correspondent areas. Ryegrass, *Poa*, and white clover accounted for 0.53 ± 0.028; 0.06 ± 0.016; and 0.007 ± 0.006; 0.476 ± 0.016; 0.039 ± 0.009; and 0.0161 ± 0.006; 0.492 ± 0.007; 0.044 ± 0.008; and 0.017 ± 0.005 of the total live tissue in the areas of tall and short vegetation and on the whole areas weighted for proportions respectively. The proportion of lamina in the areas covered by tall vegetation and on the whole sward was higher at the 1900 than at the 1600 herbage mass (0.41 vs 0.35 ± 0.022 and 0.38 vs 0.33 ± 0.005, $P < 0.05$) but it was not affected by animal species. The proportion of attached dead was not affected by either herbage mass or animal species and it accounted for 0.165 ± 0.051; 0.178 ± 0.031 and 0.175 ± 0.028 of the total in tall and short areas and for the weighted mean, and the same was observed in tall and weighted estimation of litter proportion 0.169 ± 0.077; 0.117 ± 0.043. However in the short vegetation areas the proportion of litter was higher at the 1600 mass than the 1900 mass (0.210 vs 0.171 ± 0.0137, $P < 0.05$). Extra details on sward botanical composition are given in Tables A4.1 to A4.4, Appendix A4.

Vertical Distribution of the Herbage Mass

The proportional distribution of lamina, stem and dead tissue throughout the vertical profile is depicted in Figure E4.2 and Table A4.5. The proportion of lamina in the horizon 0-2 cm from the

ground level was higher at the 1600 than at the 1900 herbage mass (0.34 vs 0.24 ± 0.027, $P < 0.05$) but stem and dead tissue proportions were not affected by either herbage mass or animal species. However in the 2-4 cm horizon the effect of herbage mass on lamina proportion was in the reverse direction (0.16 vs 0.23 ± 0.017, $P < 0.05$) and the proportion of lamina was higher in cattle- and sheep- than in mix-stocked swards (0.208 vs 0.207 vs 0.170 ± 0.021, $P < 0.05$). In the 4 to 6 cm horizon the lamina proportion was higher at the 1900 mass than at the 1600 mass (0.109 vs 0.054 ± 0.015, $P < 0.05$). The other two components were not affected by either herbage mass or animal species, throughout the vertical profile.

Species Population Densities

Mean species tiller population density in the tall and short areas and the mean for paddocks as a whole weighted for the proportion of tall and short areas are presented as block diagrams (Figures E4.3, E4.4 and E4.5 and Tables A4.6, A4.7 and A4.8, Appendix A4).

Clover contribution was lower than 5% of the total population in all the treatments, and the number of active meristems for this species are shown on a different scale to that used for grass tillers.

In June, the paddocks to which sheep treatments were allocated tended to have greater tiller densities than the other paddocks (Figure E4.5a) but the differences were not significant. This period was used as a covariate in the analysis of the September population densities, but the covariate effect was not significant ($P < 0.05$) so the unadjusted mean effects are presented here.

In September, the total population in the areas covered by tall vegetation (Figure E4.3a) was similar at the 1600 and at the 1900 mass, but in October it was higher at the 1600 than at the 1900 mass (31500 vs 20400 ± 1700 tillers m^{-2}, $P < 0.05$) however it was not affected by animal species. Ryegrass tillers (Figure E4.3b) accounted for 0.8-0.9 of the total for all treatments, so densities for ryegrass are very similar to total population density. Poa and white clover populations (Figures E4.3c and d) were not affected either by herbage mass or animal species, and they remained constant between sampling dates.

Total and ryegrass population densities on the areas covered by short vegetation (Figure E4.4a and E4.4b) were similar at both levels of herbage mass in September but by October the population was higher at the 1600 mass ($P < 0.05$). Total and ryegrass population densities under cattle grazing were lower than under mixed or sheep grazing (20900 vs 25300 vs 25500 ± 1040, and 24000 vs 28400 vs 29700 ± 1200 tiller m^{-2}, $P < 0.05$). Poa and white clover populations were not affected by time or animal species or herbage mass, although white clover was higher in October than in September (610 vs 420 ± 53 active meristems m^{-2}).

Total tiller populations were very low in June before treatments were allocated (16400 ± 1560) but tiller densities weighted for the proportions of tall and short vegetation areas (Figure E4.5a and E4.5b) remained constant throughout the winter until the following spring. The effect of herbage mass on the total weighted population was not significant in September but in October the weighted population was higher at the 1600 than at the 1900 mass (30000 vs 232000 ± 1300 tillers m^{-2}, $P < 0.05$).

This difference disappeared over the winter. Total tiller population was not affected by animal species.

Tiller Weight

Ryegrass tiller weights calculated from 40 tillers per plot in areas covered by tall and short vegetation are summarised in Table E4.5. Tillers from the areas covered by tall vegetation were heavier than tillers from the short areas (17.9 vs 9.4 ± 0.62 mg dm tiller^{-1}, $P < 0.05$) and tillers from the 1900 were heavier than those from the 1600 sward (14.7 vs 12.6 ± 0.62 mg dm tiller^{-1}, $P < 0.05$).

Weights of the tiller and active meristems for tissue turnover estimates in the areas covered by tall and short vegetation and weighted for the proportions of both are summarised in Table E4.6, E4.7 and E4.8 for ryegrass, *Poa* and white clover respectively. For the two grasses in the tall areas the interaction animal species x herbage mass was significant ($P < 0.05$). Clover active meristems however, were heavier at the 1900 than at the 1600 herbage mass (23.6 vs 15.9 ± 1.8 mg dm active meristem^{-1}, $P < 0.05$) and they were heavier in cattle- than in mix- or sheep-stocked swards (28.6 vs 16.0 vs 14.6 ± 2.2 mg dm active meristem^{-1}, $P < 0.05$). In the short areas the animal effect was not significant, but the ryegrass tillers and white clover active meristems were heavier at the 1900 than at the 1600 herbage mass (14.8 vs 9.8 ± 0.73; 12.4 vs 7.4 ± 1.20 mg dm active meristem^{-1}); although *Poa* tillers followed a similar trend, the differences were not significant.

Tiller Turnover

The rates of tiller appearance, disappearance and net change were estimated, for ryegrass only, from observations made on the

cohorts of at least 20 tillers or from the single tillers. The three rates were also calculated, for each species, from the 12 tillers or active meristems marked in the areas covered by short vegetation in each plot to study tissue turnover.

The rates are quoted in relative terms (tillers.100 tillers^{-1}. day^{-1}). Analyses of variance were carried out on the rates transformed to logarithms as well as on the untransformed rates. The transformation was decided on the same basis as for Experiment 3, but, since there were no differences in the conclusions drawn from the two sets of analyses, the results presented here are based on the untransformed data.

The cohort and the single tiller techniques ran in parallel for three weeks, and then the single tillers were observed for a further five weeks. For comparative purposes the rates calculated from single tillers are presented for the first three weeks and then for the whole 8 weeks period.

Rates of appearance, disappearance and net change calculated from the cohorts of 20 tillers are presented in Figure E4.6 and Table A4.9. Neither herbage mass nor animal species had a significant effect on appearance and disappearance rates. However, net appearance rate was highest in mix- followed by sheep- and then cattle-stocked swards (1.3 vs 0.7 vs 0.4 ± 0.6 tillers.100 tillers^{-1}day^{-1}, $P < 0.05$) and it was higher at the 1900 than at the 1600 herbage mass (1.1 vs 0.5 ± 0.16 tillers.100 tillers^{-1} day^{-1}, $P < 0.05$).

The rates calculated from individual marked tillers during the eight weeks following the marking date are depicted in Figure E4.7a, b and c respectively. In all swards the appearance rate was high

in the first week of observation, it was relatively stable until the 5th week and then gently declined towards the end of the period. Appearance rate in the sheep-grazed sward at the 1600 mass was always higher than in the other swards.

The rates over the first three weeks and over the 8 weeks of measurement are summarised in Figure E4.8.1 and 2 and Table E4.10.1 and 2. Over the first three weeks the rate of tiller appearance was higher in the 1600 mass sward grazed by sheep than in the other swards, but the herbage mass x animal species interaction was not significant. Disappearance rate was higher at the 1600 than at the 1900 herbage mass (0.07 vs 0.2 ± 0.14 tillers.100 tillers^{-1}.day^{-1}, $P < 0.05$) and it was the highest in cattle- followed by mix-stocked swards and then the sheep-stocked swards (0.8 vs 0.5 vs 0.1 ± 0.17 tillers.100tiller^{-1}.day^{-1}, $P < 0.05$). However the interaction herbage mass x animal species was almost significant as a result of the high rate of disappearance in the 1600 cattle-grazed sward (Figure E4.8.1). Over the 8 weeks the tiller appearance rate was unaffected by either herbage mass or animal species but disappearance rate was higher at the 1600 than at the 1900 mass (0.7 vs 0.2 ± 0.16 tillers.100 tillers^{-1}.day^{-1}, $P < 0.05$). The rate of net change in tiller numbers was higher in sheep- than in mix or cattle-stocked swards (2.8 vs 1.3 vs 0.9 ± 0.5 tillers.100 tillers^{-1}.day^{-1}, $P < 0.05$ for cattle-, sheep- and mix-stocked swards respectively).

Tiller turnover rates calculated from the tillers marked for tissue turnover are summarised in Figure E4.9a, b and c and Tables A4.11a, b and c for ryegrass, *Poa* and white clover respectively. All the three rates were higher in *Poa*, followed by ryegrass and then white clover (11.2 vs 5.4 vs 3.6 ± 0.65; 4.2 vs 1.7 vs 0.6 ± 0.5

and 7.0 vs 3.7 vs 3.0 ± 0.90 tillers.100 tillers^{-1}.day^{-1}, $P < 0.05$ for appearance, disappearance and net appearance rate respectively) but the interaction herbage mass x animal species was significant ($P < 0.05$) for appearance and disappearance rates and the interaction plant species x herbage mass was significant ($P < 0.05$) for all rates. Overall appearance rate was lower at the 1900 herbage mass, but in *Poa* it was higher at the 1900 than at the 1600 mass.

Overall disappearance rate was higher at the 1600 than at the 1900 mass (3.2 vs 1.1 ± 0.41 tillers.100 tillers^{-1}.day^{-1}, $P < 0.05$). But the high rate of disappearance for *Poa* at the 1600 and the low rate for clover at the 1900 mass were responsible for the interaction herbage mass x plant species being significant. Animal effects were not significant for any rate.

Frequency of Defoliation

The frequency of defoliation (no. defoliations.day^{-1}) for tillers in the tall areas is given in Table E4.9A and the interval between defoliations is given in Table A4.12A. The three-factor and all the two-factor interactions were significant ($P < 0.05$).

Ryegrass tillers in the tall areas at the 1600 mass were more frequently defoliated by sheep and by cattle + sheep than by cattle (0.21 vs 0.14 vs 0.10 ± 0.030 defoliations day^{-1}, $P < 0.05$). However, the differences were not significant for the tall areas at the 1900 mass. A similar pattern was observed for *Poa* and white clover in the tall areas at the 1600 herbage mass (0.22 vs 0.17 vs 0.12 and 0.21 vs 0.05 vs 0.05 ± 0.030 defoliation day^{-1} for *Poa* and clover respectively, $P < 0.05$); at the 1900 mass the differences in frequency of defoliation between animal species were not significant for *Poa* but they were significant for white clover

(0.224 vs 0.150 vs 0.058 ± 0.030 defoliations day^{-1} for mix- cattle- and sheep-grazing respectively, $P < 0.05$).

The frequency of defoliation for the short areas is given in Table E4.9B and the interval between defoliations is given in the Table A4.12B. The three-factor plant species x animal species x herbage mass interaction was significant ($P < 0.05$). Ryegrass tillers in the short areas at the 1600 mass were defoliated at the same frequency by cattle as by sheep or sheep and cattle but at the 1900 mass frequency of defoliation was higher in the mix-followed by the cattle- and the sheep-stocked swards (0.18 vs 0.13 vs 0.10 ± 0.020 no.def.day^{-1}, $P < 0.05$). For both *Poa* and white clover, differences in frequency of defoliation were not significant either at the 1600 or 1900 herbage mass.

Tissue Turnover

Tissue turnover rates are presented at the same three levels of detail as in Experiment 3, i.e. primary unit, plant species per unit area, and combined species per unit area. In addition, mean effects are presented for areas covered by tall and short vegetation and for the total sward weighted for the respective proportions of tall and short areas. Growth, senescence and net growth rates per primary unit for perennial ryegrass, *Poa* and white clover are depicted in Figures E4.10, E4.11 and E4.12 and Tables A4.13, A4.14 and A4.15 respectively.

In the tall areas the interaction plant species x animal species was significant ($P < 0.05$) for the three rates; for grass none of the interactions were significant in the short areas but in the weighted rates plant species x animal species interaction was significant ($P < 0.05$) for growth and lamina senescence rates.

In the tall areas the growth rate was highest for clover followed by ryegrass and then *Poa* (839 vs 627 vs 302 ± 59.8 µg dm tiller^{-1} day^{-1}, $P < 0.05$). Senescence rate was highest for ryegrass followed by *Poa* and white clover (291 vs 142 vs 100 ± 25.6 µg tiller^{-1} day^{-1}, $P < 0.05$). Net growth rate followed a similar pattern to growth rate i.e. clover the highest followed by ryegrass and *Poa* (739 vs 336 vs 159 ± 65.5 µg dm tiller^{-1} day^{-1}, $P < 0.05$).

Growth rate in the short areas was higher for white clover than ryegrass and *Poa* (363 vs 310 vs 247 ± 21.4 µg tiller^{-1} day^{-1}, $P < 0.05$) and it was higher at the 1900 than at the 1600 mass (376 vs 252 ± 27.1 µg dm tiller^{-1} day^{-1}, $P < 0.05$). Senescence rate was similar for the three plant species but it was higher at the 1900 than at the 1600 mass (108 vs 72 ± 10.2 µg dm tiller^{-1} day^{-1}, $P < 0.05$). Net growth rate followed a similar pattern to gross growth rate i.e. higher rates for clover and ryegrass than for *Poa* (277 vs 227 vs 147 ± 22.3 µg dm tiller^{-1} day^{-1}, $P < 0.05$) and higher at the 1900 than at the 1600 mass (268 vs 166 ± 22.5 µg dm tiller^{-1} day^{-1}, $P < 0.05$).

Gross growth rate weighted for tall and short areas followed the same pattern as in short areas i.e. the highest for clover followed by ryegrass and then *Poa* (514 vs 395 vs 278 ± 26.4 µg dm unit^{-1} day^{-1}, $P < 0.05$) and higher at the 1900 than at the 1600 mass (480 vs 311 ± 23.6 µg dm unit^{-1} day^{-1}, $P < 0.05$).

Lamina senescence rate was higher for ryegrass than for *Poa* and white clover (157 vs 114 vs 95 ± 11.5 µg dm unit^{-1} day^{-1}, $P < 0.05$) and it was higher at the 1900 than at the 1600 mass (156 vs 88 ± 10.7 µg dm unit^{-1} day^{-1}, $P < 0.05$).

Net growth followed the same pattern as gross growth, the rate being higher for clover than for ryegrass and *Poa* (419 vs 238 vs 163 ± 28.8 µg dm unit^{-1}day^{-1}, $P < 0.05$) and it was higher at the 1900 than at the 1600 mass (325 vs 222 ± 23.5 µg dm unit^{-1} day^{-1}, $P < 0.05$).

The three rates per unit area for ryegrass, *Poa* and white clover in the tall areas are summarised in Figures E4.13A, E4.14A and E4.15A and Tables A4.16A, A4.17A and A4.18A. The three-factor plant species x animal species x herbage mass interaction was significant ($P < 0.05$) for gross growth rate and senescence rate and the plant species x animal species and herbage mass x plant species interactions were significant for senescence, but none of the interactions were significant for net growth rate. In the tall areas, the three rates were highest in ryegrass followed by *Poa* and white clover (127.5 vs 11.6 vs 1.8 ± 6.4; 56.0 vs 4.7 vs 0.2 ± 3.7 and 71.6 vs 6.8 vs 1.6 ± 7.8 kg dm.ha^{-1}day^{-1}, $P < 0.05$, for gross growth, senescence and net growth rate respectively). The herbage mass or animal species effects were not significant, the exception being that the rate of senescence was higher for ryegrass in the tall areas at the 1900 mass (76.6 vs 35.3 ± 3.0 kg dm ha^{-1} day^{-1}, $P < 0.05$).

The rates in the short areas followed the same species pattern as in the tall areas, i.e. the highest rates for ryegrass followed by *Poa* and white clover (64.9 vs 5.0 vs 1.4 ± 3.4; 14.2 vs 1.5 vs 0.3 ± 0.7 and 53.2 vs 5.1 vs 1.3 ± 2.8 kg dm ha^{-1}, $P < 0.05$ for gross growth, senescence and net growth respectively). However the two-factor herbage mass x plant species interaction was significant ($P < 0.05$) for all the three rates and the plant species x animal

species interaction was significant ($P < 0.05$) for growth rate. The three rates for ryegrass were higher at the 1900 than at the 1600 mass (79.8 vs 50.0 ± 2.8; 16.6 vs 11.7 ± 0.7 and 63.2 vs 38.3 ± 2.8 kg dm ha^{-1} day^{-1}, $P < 0.05$) but the herbage mass effect was not significant for the other plant species.

The three rates weighted for the proportion of tall and short areas were all highest for ryegrass followed by *Poa* and then white clover (82.6 vs 7.6 vs 1.6 ± 3.3; 29.4 vs 2.6 vs 0.3 ± 1.4 and 53.2 vs 5.1 vs 1.3 ± 3.4 kg dm ha^{-1} day^{-1}, $P < 0.05$ for gross growth, senescence and net growth respectively), but the two-factor herbage mass x plant species for growth and senescence and the plant species x animal species for senescence rate were significant ($P < 0.05$). None of the interactions were significant for net growth. Both growth and senescence rates for ryegrass (Figure E4.13C) were higher at the 1900 than at the 1600 mass (98.7 vs 66.4 ± 8.2 and 40.4 vs 18.4 ± 3.3 kg dm ha^{-1} day^{-1}, $P < 0.05$). The senescence rate was highest in mix-stocked swards, followed by sheep- and cattle-stocked swards (36.8 vs 30.8 vs 20.6 ± 2.3, $P < 0.05$). Net growth was not affected either by animal species or herbage mass.

Rates of growth, senescence and net production in tall and short areas and weighted means for combined species per unit of area are summarised in Figure E4.16A, B and C and Tables A4.19A, B and C respectively. The growth rate in the tall areas in cattle-grazed swards at the 1900 mass was very low, but the herbage mass x animal species interaction was not significant. The rate of lamina senescence was higher at the 1900 than at the 1600 mass

(81.2 vs 40.5 ± 9.1 kg dm ha^{-1} day^{-1}, $P < 0.05$). The net production rate followed the same pattern as gross growth rate and the herbage mass x animal species interaction was not significant.

Total growth and net production rates in the short areas (Figure E4.16B) were higher at the 1900 than at the 1600 mass (88.2 vs 43.5 ± 7.0 and 69.3 vs 41.3 ± 8.4 kg dm ha^{-1} day^{-1}, $P < 0.05$).

Total growth and senescence rates weighted by tall and short areas (Figure E4.16C) were higher at the 1900 than at the 1600 mass (116.4 vs 75.2 ± 10.9 kg dm ha^{-1} day^{-1} and 43.6 vs 20.8 ± 2.0 kg dm ha^{-1} day^{-1}, $P < 0.05$) and senescence rate was higher in mix- and sheep-stocked swards than in cattle-stocked swards (38.5 vs 34.9 vs 23.3 ± 2.5 kg dm ha^{-1} day^{-1}, $P < 0.05$). However the differences in net production due to either herbage mass or animal species although substantial were not significant.

Stratified sampling efficiency

The precision gained from stratified sampling compared to random sampling for each variate involved is shown in Table E4.10. The precision gained is shown as the reduction in the variance weighted by the proportion of each stratum and expressed as proportion of the weighted variance (Sukhatme and Sukhatme 1970).

There were only marginal advantages for stratified sampling in three of the eight parameters analysed, and in the other five there was some loss of precision in estimating variance.

Animal Measurements

For digestibility and intake per animal and botanical composition

of the diet the pooled standard errors of the mean were calculate by analysis of variance within species, because the variance in cattle was greater than in sheep ($P < 0.05$).

Stocking Rates

The stocking rates necessary to maintain swards at a constant sward surface height are given in Table E4.11. The linear regression between cattle (x) and sheep (y) stocking rates in single and in mixed-stocked treatments was described by the equation E4.1.

$$Y = 3.7X - 0.8 \quad r^2 = 0.957 \; n = 8 \qquad \text{E4.1}$$

Table E4.11. Stocking rate (animals/ha) in swards grazed by cattle, sheep and by both species together.

HM/Animal Sp.	Cattle	Sheep	Cattle+Sheep
1600	13.3	48.2	6.2 + 18.5
1900	5.7	24.8	3.3 + 9.9

Diet Digestibility

The treatment mean values for organic matter digestibility of the extrusa samples are given in Table E4.12. The digestibility of herbage selected by cattle alone or in combination was higher at the 1900 than at the 1600 mass (0.73 vs 0.69 $\pm$ 0.005, $P < 0.05$ cattle single vs mixed species), but the digestibility of the diet was not affected by the presence of companion species in either cattle or sheep.

Herbage Intake

The herbage intakes (g OM animal^{-1} day^{-1}) of cattle and

Table E4.15. Components of the diets selected by cattle (I) and sheep (II) grazing alone or together (proportion).

I Cattle

Herbage Mass/Component animal sp.	Lamina		Stem		Dead		Roots	
	C	C+S	C	C+S	C	C+S	C	C+S
1600	0.72	0.67	0.11	0.12	0.10	0.14	0.07	0.07
1900	0.86	0.84	0.06	0.07	0.06	0.06	0.02	0.02
$SE\bar{x}$		0.033		0.010		0.016		0.013

II Sheep

Herbage Mass/Component animal sp.	Lamina		Stem		Dead		Roots	
	S	S+C	S	S+C	S	S+C	S	S+C
1600	0.93	0.82	0.02	0.09	0.04	0.03	0.01	0.03
1900	0.93	0.93	0.02	0.02	0.03	0.04	0.01	0.01
$SE\bar{x}$		0.018		0.011		0.004		0.005

sheep are summarised in Table E4.13. Intakes were higher in both cattle and sheep grazing alone or in mixture at the 1900 than at the 1600 mass, both in absolute terms (4480 vs 3610 ± 206.7 and 1040 vs 780 ± 50.0 g OM animal^{-1} day^{-1}) and per unit live weight (16.2 vs 14.4 ± 0.483 g OM kg LW^{-1} day^{-1}, $P < 0.05$). The reduction of intake due to herbage mass tended to be higher in both species when grazing together than when grazing alone.

Total herbage consumption per hectare for all the treatments is summarised in Table E4.14. The total harvested was higher at the 1600 than at the 1900 mass (41.4 vs 31.1 ± 1.4 kg OM ha^{-1} day^{-1}, $P < 0.05$), and was higher for cattle and mixed populations than for sheep alone (39.3 vs 29.4 vs 40.2 ± 1.70 kg OM ha^{-1} day^{-1}, $P < 0.05$ for cattle and sheep and combined species respectively).

Botanical Composition of the Diet

The proportion of lamina, stem, dead tissue and roots components in the extrusa samples are given in Table E4.15. The proportions of clover were less than 0.01 for both cattle and sheep and are not presented here. The proportion of grass lamina in the extrusae collected from cattle was higher at the 1900 than at the 1600 mass (0.85 vs 0.69 ± 0.024, $P < 0.05$) but stem, dead and roots proportions were lower (0.07 vs 0.12 ± 0.007 and 0.06 vs 0.12 ± 0.011 and 0.02 vs 0.07 ± 0.009, $P < 0.05$ respectively).

The proportion of lamina, dead tissue and root proportion in the extrusae collected from sheep followed a similar pattern to those collected from cattle (0.93 vs 0.88 ± 0.012; 0.06 vs 0.04 ± 0.003 and 0.017 vs 0.01 ± 0.004, $P < 0.05$), but the proportion of the stem was higher in the extrusae from the 1600 than from the

1900 mass (0.06 vs 0.03 ± 0.008, $P < 0.05$).

For lamina proportions the interaction herbage mass x sheep grazing alone or with cattle was significant, the proportion being lowest in the extrusa samples selected by sheep grazing with cattle at the 1600 mass (Table E4.15). The dietary overlap indices (Morisita, 1959 and Horn, 1966) are given in Table E4.16. These indices indicated that the diets of cattle and sheep overlapped completely, whether the animals grazing separately or in combination.

DISCUSSION

Statistical Procedures

The experiment had two replicates in space and six treatments so 5 degrees of freedom were available to estimate the residual variance (Table D4.1). Between-treatment differences in the rate of net herbage production which were twice the size of those in Experiment 3 were not significant at $P < 0.05$. Thirty five degrees of freedom would have been needed to demonstrate significant differences between animal species in the analysis for net herbage production weighted for the proportion of the grazed and ungrazed areas (Table D4.1) or twenty degrees of freedom on the areas covered by short vegetation alone (Table D4.2).

Stratified sampling did not improve precision in the estimate of the residual variance compared with random sampling (Table E4.10) because the variance in tall areas was higher than expected. In fact the assumption of equal variances within areas covered by tall and short vegetation (stratum) was made when the numbers of samples per stratum were allocated. The other reason why stratified sampling failed to improve the precision of estimating

the residual variance was because the probable size of the areas covered by tall vegetation was under-estimated. The estimate of the areas covered by the two kinds of vegetation was made from estimates in Experiment 3 (A. Huber, personal communication). The proportion of ungrazed area in a paddock was higher in the present experiment however, particularly at the 1900 mass. In order for benefits to accrue from stratified sampling a higher number of observations should have been taken from areas covered by tall vegetation.

From the current experiment it seems that all the alternatives to reduce residual variance may involve much more labour and material than may readily be available, so there will be justification to look for alternative experimental designs. The unreplicated experiment approach, as in Experiment 3, involving more treatments, may be one alternative but it involves the risk of confusing treatment effects with natural differences. The use of unreplicated experiments using the animal rather than the herd as experimental unit has been suggested by Morley and Spedding (1968) as a desirable procedure for saving resources under rotational grazing. Coniffe (1976) has shown that, using this approach, the conclusions drawn may not be seriously affected, and on the same grounds an approach of using a smaller division than a paddock on rotational grazing may be supported.

However, under continuous grazing the subdivision of plots into small areas does not allow one to estimate the contribution of the different areas to the variance because the division is merely notional. That is not to suggest that the treatment effects

shown to be significant from unreplicated designs are not real treatment effects. Sward experiments carried out at this Institute using unreplicated designs have consistently shown similar patterns of response in herbage production to variation in sward conditions (Bircham and Hodgson, 1981; S.A. Grant, personal communication). By using the same amount of resources as were required for Experiment 4, information could be obtained from the same three animal treatments over four levels of herbage mass in an unreplicated design, allowing responses to be estimated by regression techniques and comparisons made between regression lines (Morley, 1978). This approach would have potential advantages in some situations, especially when the main requirement is to establish general patterns of response. However, similar problems created by few degrees of freedom may be expected when the mean square of the deviation from the fitted values is estimated for comparisons between regressions.

From the above discussion there does not appear to be any way to estimate reliable residual variations of the components of tissue turnover to compare mean treatment effects under continuous stocking management which does not make heavy demands on resources. Replication in time or in different regions of experiments may be the best alternative, but too many other factors vary from year to year or region to region. Despite these reservations, the differences in net herbage production observed in Experiment 4 are considered to be real treatment effects rather than random differences.

Proportion of Area Covered by Tall Vegetation

Areas covered by tall vegetation associated with dung

deposition have been reported to occupy between 0.1 and 0.45 of the total area for beef and dairy cattle grazing in a wide range of conditions (see Marsh and Campling, 1970) but there are no published estimates of the areas rejected by grazing sheep. In Experiment 3 the proportion of a paddock under-utilised was 0.33 of the total area at both herbage masses grazed by sheep, and ranged from 0.16 to 0.40 of the area in cattle-grazed swards. In the present experiment the proportion of area covered by tall vegetation increased with herbage mass and it was higher in sheep-grazed swards (Table E4.2). Overall the estimates of area rejected were higher than in Experiment 3, but if some allowance is made for differences in herbage mass and different methods between the experiments, the estimates may be regarded as equivalent. The herbage mass in tall areas was not affected by animal species or overall herbage mass, because the tallest under-grazed areas in the cattle-grazed sward at 1900 had less tillers than the undergrazed areas in sheep swards or mix-stocked swards (Figure E4.3). These results do not support the suggestion by Nolan (1980) that mixed stocking may reduce the amount of herbage on, and the proportion of under-grazed areas. However, the tall areas on the different treatments did not have similar patterns of tissue turnover (see later).

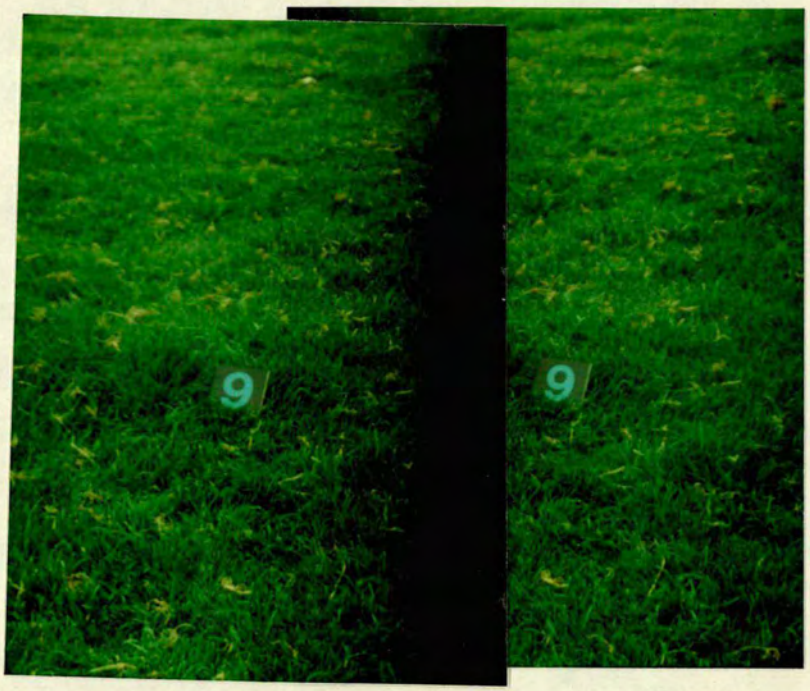
Herbage Mass

The differences in herbage mass and in sward surface height between animal species were not significant, but the prescribed differences between treatments within species were achieved (Table E4.3). There appeared to be a good agreement

between sward surface height and the actual herbage mass, although herbage mass was estimated as the average weighted for proportion of areas covered by tall and short vegetation, whilst sward surface height was the average of random observations. The mean sward surface height of the population calculated from random samples may have under or over-estimated the mean weighted height of the sward surface, and this bias may be expected to increase as the departure from the equal proportion of grazed and ungrazed areas increases. However, the sward surface height was used to give quick estimates of the herbage mass on which the adjustments in animal numbers were based, and this purpose seems to have been achieved without increasing complexity in the procedures.

Variation in Sward Surface Height

Variation in sward surface height has normally been considered in terms of the difference in variability between grazed and cut swards, and has been associated with possible differences in the dynamics of herbage growth (Spedding, 1971; Smith *et al*, 1975). Differences in the variance of sward surface height between cattle- and sheep-grazed swards were evident early in the grazing season but disappeared after 110 days of grazing (see Experiment 3). In the present experiment the effect of the grazing animal on the variance of the sward surface height developed gradually and by the end of August (45 days after treatments were allocated) the variation in sward surface height was greater on cattle-grazed swards (Table E4.4). This result is in line with observations made in the second period in Experiment 3, (75 days after treatments were allocated). However, in Experiment 3 differences disappeared by the end of the season. Unfortunately the objective observations



3) mix-stocking

Plate E4.2. Stereo photograph of dung patches in cattle, sheep and mix-stocked swards (a simple stereoscope will aid viewing).

for estimates of variance in sward surface height at the end of the season were not made in the current experiment. However the subjective impression was that the variability of sward surface height decreased within and between swards towards the end of the season. Visual estimates showed that areas of tall vegetation in cattle-grazed swards were well delimited and much taller than the average of the vegetation (Plate E4.2.1) and that they were shorter but more diffuse in sheep-grazed swards (Plate E4.2.2) whilst in mix-stocked swards they were intermediate in character (Plate E4.2.3).

The intermediate variance of the sward surface height in the mixed-stocked swards may be the result of a more efficient use of herbage in the vicinity of the dung pats than on the cattle-grazed swards. Alternatively an intermediate variance may be the consequence of fewer tall areas being created by cattle as a proportion of the total. Nolan (1981) has reported that sheep spent a longer time grazing on tall areas of vegetation while cattle refused to do so. However, Forbes (1982) showed that cattle were very sensitive to their own dung but relatively insensitive to sheep dung, whilst sheep were relatively insensitive to both cattle and their own dung. Both authors suggest that lower wastage of herbage round dung patches may occur under mix-stocked systems, at least compared with cattle-stocked systems. This possibility of increasing the efficiency of use of undergrazed areas with mixed-stocking should be reflected in a higher frequency of defoliation of tillers in the tall areas. In the present experiment, however, the overall frequency of defoliation of individual units

in the tall areas in mix-stocking swards was similar to the frequencies in sheep and cattle-swards (Table E4.9a).

The evidence indicates that mixed stocking may have resulted in greater efficiency of herbage utilisation than that observed under cattle grazing, but that it did not offer any advantage over sheep grazing.

Sward Botanical Composition

The swards were ryegrass dominant, the companion *Poa* and white clover amounting to less than 0.1 of the total mass (see page 172) and between 0.1 and 0.2 of the total population (see page 177). The botanical composition was uniform across treatments both on the total sward and in terms of the vertical distribution of herbage (Figure E4.2). The proportion of lamina in the upper layers of the canopy decreased with herbage mass but the reverse was observed in the layer 0-2 cm from ground level. As the total number of contacts was the same for each treatment (200 contacts) the proportions give an estimation of the density of the sward in each horizon. The higher density of leaves in the upper horizons of the taller sward was reflected in a higher lamina proportion in the diets selected by both animal species from these swards (Table E4.15).

Species Population Dynamics

The high proportion of ryegrass tillers in the areas covered by both tall and short vegetation suggest that the sward may be regarded as a ryegrass population with little interference from other plant species. A low proportion of *Poa* was expected since its penetration into ryegrass swards after high density sowing is very unlikely (Wells, 1974). The low proportion of clover,

may have been the consequence of high mortality during the winter after sowing (J. Rogers,personal comunication).

In all swards there was a significant increase in tiller numbers from June to September (Figure E4.5). The low tiller number in June may have been the consequence of the field having been closed for conservation during May to the end of June. Depressions in tiller density in swards left to grow undisturbed are to be expected because of self thinning largely as a consequence of competition for light (Yoda *et al*, 1963; Kays and Harper, 1974). Such thinning after even short periods of time have been described by Davies (1977) and by Bircham (1981a), and dramatic losses of tillers in swards closed for conservation have been described by Williams (1970). Some of the tiller buds previously inhibited may have been released, after cutting, resulting in an increase in tiller numbers (Davies, 1977).

In September there were similar tiller populations in tall and short areas (compare Figure E4.3 with E4.5). This may be expected since the tall areas were of recent formation. The estimates were made five weeks after grazing started and self-thinning mechanisms may not have acted long enough to reduce tiller numbers. In fact when tillers are shaded below the compensation point on spaced plants, tiller death may be delayed up to 60 days if the rest of the plant is illuminated, though some tillers may die after 21 days of heavy shade if the rest of the plant is heavily shaded (Ong and Marshall, 1979). The fact that tiller density on tall areas in October was lower at 1900 than at the 1600 mass gives some support to the above view. Although areas

covered by tall vegetation are dynamic, it is more likely that old dung patches persisted for longer at the low than at the high grazing pressure (Norman and Green, 1958). Tall areas had lower tiller densities on cattle swards than on the other treatments (Figure E4.3). This may be the reflection of lower tiller density in the grazed areas (Figure E4.4), or a consequence of the areas being older because of a high sensitivity of cattle to their own dung (Forbes, 1982), or a combination of both. In short areas, both animal species effects and herbage mass effects developed from September to October. By October tiller populations were lower in cattle-grazed swards and higher at the 1600 mass, in line with Experiment 3 and other published evidence (Boswell and Crawford, 1978; Briseno de La Hoz and Wilman, 1981; Bircham and Hodgson, 1981; Tallowin, 1981). The differences between animal species may be explained by higher tiller disappearance rates in cattle-grazed swards, whilst differences between herbage masses were the result of the high appearance rate at 1600 mass (Figure E4.8.2 and E4.9a).

The weighted average tiller density followed a similar pattern to the population in the grazed areas, but the differences between animal species were not significant. The magnitude of the differences in the weighted means, however, was similar to those in the grazed areas (Tables A4.6 , A4.7 and A4.8) and the lack of significance may be attributed to a higher residual variance estimated from the weighted analysis. The low number of replicates and the failure to gain precision by using stratified sampling in estimating the residual variance, as discussed in page 210 , may both have contributed to the high residual variance estimated from the weighted analysis.

Tiller Weight

Wade (1979) has suggested that the possible tendency to choose tillers from the edge of plants within a sward may introduce some degree of bias to estimates of tiller turnover and tissue turnover rates. Tillers from the edge of a plant may receive more light and consequently may be larger than the average and, as shown in Experiment 2, elongation rates are higher on the bigger tillers. In the current experiment the weight of the marked tillers in the areas covered by short vegetation was similar to the weight of tillers selected at random from a set of independent samples, where the risk of choosing the bigger tillers may have been lower (Tables E4.5b and E4.6b). However, there was a poor agreement between tiller weight selected from these samples and those marked in ungrazed areas (Tables E4.5A and E4.6A). These results suggest that estimates of the rates of tissue turnover for the areas covered by tall vegetation may have been over-estimated in some treatments and under-estimated in others. The likely bias in selecting tillers on the tall areas may help to explain some of the interaction discussed in the next section.

Tiller Turnover

Fluxes of tillers are important in relation to patterns of persistency and survival, but there is relatively little information on measurements of tiller turnover under grazing. The objective in comparing measurement techniques was to widen experience of the estimation and analysis of tiller turnover.

Observation on the single tillers and on the cohorts of 20 tillers gave slight differences in the absolute estimates

of the rates, but both techniques gave a lower net appearance rate in cattle-grazed swards (Figures E4.6 and E4.8) and this result is in line with that of Experiment 3. The high rate of net tiller appearance calculated from the cohort technique for mix-stocked swards at the 1900 mass is difficult to explain, since it was the result of an unexpectedly high rate of tiller appearance. However, though the high rates of tiller appearance in the mixed and sheep-stocked swards at the 1900 mass seem to be at variance with estimates from Experiment 3, they were in general agreement with rates calculated from the single tillers over the same period (see below).

Estimates from the single tiller technique were high in the first week, then remained relatively constant for four weeks, and then declined towards the end (Figure E4.7). The rate of tiller appearance at the 1600 mass grazed by sheep was exceptionally high over all the 8 weeks. The abnormal rate was mainly associated with very high values in two quarters of a paddock, and this suggests that other causes rather than treatment effects may be responsible. The initially high rates over all treatments may well have been the result of a bias brought about by a tendency to mark more tillers from the edge than from the centre of plants as suggested by Wade (1979) and this effect might have been diluted over a large number of tillers. When the low number of tillers was compensated for by a longer period of observation (Figure E4.8.2), tiller appearance rate was still high on the sheep 1600 treatment but the initial effects were very much reduced. The abnormally high rate of tiller appearance in the sheep-grazed sward at the 1600 mass makes it

difficult to interpret the differences between treatments, and to compare techniques.

During the first three weeks of observations the rate of tiller appearance tended to be higher at the 1900 than at the 1600 mass, independent of the technique from which it was calculated. This result may be expected in the case of the single tiller estimates, since disturbances in the sward canopy when marking the tillers may have allowed more light to reach the base of the tillers resulting in more tiller buds being stimulated to develop (Mitchell and Coles, 1955). However in a cohort of 20 tillers the effects of canopy disturbances were expected to be negligible at least on the central tillers and in this case there is not a clear explanation for these unexpectedly high rates.

The rate of tiller disappearance over three weeks, estimated either by the cohort or by the single tiller technique, was greater in cattle-grazed swards and at the 1600 mass, although the differences were not always significant (Figures E4.6 and E4.8). In the single tiller technique the first tiller to disappear was observed during the third week after marking. This may be a consequence of the limited population of tillers which were marked. As discussed earlier the rates calculated over the whole period may be more realistic than rates calculated for a shorter period.

There was good general agreement between techniques in showing lower rates of net tiller appearance under cattle grazing. This observation supports the results of Experiment 3 and explains the lower tiller population densities observed under

Table D4.3. Net appearance rate of ryegrass tillers (tillers. 100 tillers^{-1} day^{-1}) calculated from (a) the difference between tiller densities in September and October, (b) single tillers, first 3^{+} weeks, (c) single tillers between 5th* and 8th weeks, (d) the cohort^{+} technique and (e) the tillers numbered for tissue turnover estimates^{O}.

		Net tiller appearance rate				
Herbage Mass	Animal Species	a	b	c	d	e
1600	C	-0.10	0.2	-0.2	0.3	4.7
	S	0.80	5.2	1.1	0.7	6.4
	C+S	0.40	0.1	0.0	0.6	2.5
1900	C	-0.80	2.6	0.4	0.5	2.2
	S	-0.05	2.6	0.4	0.7	4.4
	C+S	-0.01	1.4	0.2	2.0	1.9
$SE_{\bar{x}}$		-	1.0	0.41	0.30	2.10

$^{+}$ first three weeks in August

* during September

O first fortnight in September

cattle grazing. However, the low number of tillers on which the estimates were based make them of limited use in predicting seasonal changes in the tiller population. For this purpose the estimates from a small number of single tillers observed over a short period may over-estimate the net change. The initial over-estimate in gross appearance rate brought about by canopy disturbance as discussed earlier may be carried over into the estimation of the net rate of change.

The estimates of the rate of net population change from single tillers during September or from the cohort of 20 tillers during the first three weeks in August, came nearest to the observed changes in tiller densities (Table D4.3). Overall there was no evidence to show that one technique was better than the other, and it may be advisable to compare them over a larger number of observations before firm conclusions can be drawn. Marking a larger number of single tillers would allow demographic studies to be carried out on grazed swards, but this is not possible with the cohort technique since age classes are unidentifiable (Armitage, 1971; Callaghan, 1976; Davies, 1981).

Tissue Turnover

Species primary unit performance

The effect of dung pats on sward growth dynamics has been discussed by Nolan (1980). He remarked that under cattle rotational grazing 0.15 of the total area was under-grazed and had a net herbage accumulation rate twice as high as the grazed areas, and that this effect persisted for twelve weeks after dung deposition. As cattle reject the herbage in the vicinity of dung

pats it may be concluded that the herbage mass accumulated will eventually die, and tiller population may be reduced as a consequence of self-thinning mechanisms. In the present experiment the primary units in the tall areas grew twice as fast as the primary units in the short areas, and similar ratios may be calculated on an area base. However in cattle plots the growth per primary unit was approximately the same in tall and short areas (see Figures E4.10 a and b).

This variation in growth dynamic on the tall areas may be expected since tillers of different weight were marked in the areas in different treatments. Alternatively the lower growth rate in cattle tall areas at 1900 mass may have been the result of having marked tillers that were heavily shaded by bigger tillers growing in an old tall area (Ong and Marshall, 1979). The high rates in other tall areas may have been the result of having marked tillers in areas of recent formation, where shading between tillers may not have been heavy enough to reduce growth rate.

In the short areas the growth rate per primary unit was not affected by animal species, but it increased with herbage mass. These results confirmed those previously described in Experiment 3 and reported by other workers (De Lucia Silva, 1974; Wade, 1979; Bircham, 1981b; Grant *et al*, 1981a). The weighted average growth rates per primary unit followed similar patterns to those in the areas covered by short vegetation for both grasses and for white clover, and the growth rate per individual in tall areas merely affected the magnitude of the weighted rate (Figure E4.10).

The lamina senescence rate was higher in the tall than in the short areas (Figure E4.10A.and B). It appears to be a widely accepted concept that senescence rate increases with herbage mass because more tissue is available for senescence (Morris, 1970; Wade, 1979; Bircham and Hodgson, 1981). However, the intensity of light intercepted by the ageing leaf located at the lower layers in the canopy may have been low, and this in turn may have contributed to accelerated senescence rates (Brougham, 1958; Hopkinson, 1966). In short areas the rate of lamina senescence increased with herbage mass and the same interpretation as for the differences between tall and short areas may hold here too.

The higher rates of lamina senescence at the higher herbage masses did not balance the higher growth rate, and net growth rate followed the same patterns as gross growth rate. Animal species did not affect net growth rate per primary unit and this result confirmed those previously discussed in Experiment 3. The negligible animal effect on net growth rate per primary tiller reinforces the hypothesis suggested in page 143 that, within a herbage mass, the animal effect on the rates per unit area comes through effects on the tiller population rather than on the individual tiller.

Plant Species Performance

The swards were ryegrass dominant in numbers and consequently the contributions of the companion *Poa* (< 20 $kg.ha^{-1}.day^{-1}$) and white clover (< 3 $kg.ha^{-1}.day^{-1}$) were very low. Both *Poa* and white clover were distributed in patches and, over all treatments, 0.31 and 0.61 of the samples collected for tiller density estimates

did not have *Poa* or white clover units. This particular distribution makes the interpretation of the rates per plant population per unit area rather difficult. The combined species rates followed similar pattern to ryegrass and rates per unit area are discussed in next section.

Combined Species Per Unit Area Performance

From population densities and growth rate per primary unit in the tall areas, three different relationships between the individual and the population may be distinguished. A combination of low growth per tiller and a low number of tillers per unit area was responsible for the lowest rate per hectare in tall areas in cattle-stocked swards at the 1900 mass. The high growth rates in the tall areas in sheep-stocked swards appeared to be the result of many tillers growing at a relatively low rate. The third class of tall area was characterised by intermediate tiller densities growing at relatively high growth rates (see Figures E4.5a and E4.10a). Similar adaptive mechanisms to the two last described have been observed when swards continuously stocked and maintained in steady state are allowed to grow by reducing animal numbers (Bircham, 1981a). The absolute rates for the areas covered by short vegetation and for the weighted mean are in the same range as Experiment 3 and as values reported elsewhere (Tainton, 1974; Bircham and Hodgson, 1981). The weighted average growth rate followed a similar pattern to the rate in the short areas, but in cattle-stocked swards at 1900 mass the low rate in tall areas was reflected in a low average growth rate (Figure E4.14c). The weighted average growth rate increased with herbage mass, but though the differences in growth rate due

to animal species were twice as large as in Experiment 3, the animal species effect was not significant. The possible reasons for this have been discussed on page 210 .

Lamina senescence rates followed the expected patterns, i.e. they increased with herbage mass. One of the more interesting results was the maximum rate of 100 kg ha^{-1} day^{-1} measured in tall areas in the mixed-stocked swards at 1900 mass (Figure E4.14A). The major contribution to the high rate of senescence was from ryegrass (Figure E4.11a) but, as no further descriptive observations of these areas were made, this result cannot be generalised. However, the low weighted average rate of senescence in the cattle-stocked swards was presumably associated with low tiller density confirmed results from Experiment 3.

The rate of net herbage production was significantly higher at the 1900 than at the 1600 mass though on the basis of the evidence of Bircham and Hodgson (1981), little change would have been expected over this range. The explanation suggested previously to interpret similar results from Experiment 3 seems to hold here too. As the tiller populations were lower than those reported by Bircham and Hodgson (1981) an increasing net production rate may be interpreted as an indication that the sward had not completely filled the environment capacity (Odum, 1971).

The non-significant differences in net herbage production rate between animal species may be attributed to the low sensitivity of the analysis (see page 210), or alternatively, to the short experimental period which did not allow animal effects to be fully expressed. However, the average net herbage production rates

(51.1 vs 71.6 vs 68.1 ± 15.5 kg dm $ha^{-1}.day^{-1}$ for cattle, sheep- and mix-stocked swards respectively) suggest that it is reasonable to expect lower net production rate in cattle grazed swards. This result confirms results from Experiment 3, although in the current experiment the lower rate of net herbage production in cattle-grazed swards was largely due to a very low rate at the 1900 mass (see Figure E4.16 and Table A4.19, Appendix A4). However, in Experiment 3 the rate of net production at the high herbage mass grazed by cattle (equivalent to the 1900 mass in the present experiment) was lower than at the intermediate mass (equivalent to 1600 mass) at the end of the season. Thus it seems likely that the differences between cattle and sheep in net herbage production are more marked at low and at high levels of herbage mass than at intermediate levels.

The results of the current experiment also give support to the hypothesis that net herbage production in mix-stocked swards may be similar to those on the sheep-stocked swards. Certainly there is no indication that they are likely to be higher. Tiller densities and tissue turnover rates in the mix-stocked swards were intermediate between the values for single-stocked swards. The proportion of the two species in mix-stocked treatments was fixed at 1:1 on an intake basis but, if the proportion of one animal species is increased, tiller densities and net production rates may resemble those of the species in the highest proportion.

Herbage Consumption Per Unit Area

The rate of total herbage consumption per hectare was in reasonable agreement with the average net herbage production rate

Table D4.4. Balance between rate of herbage consumption (c) and net herbage production (np) in short areas (G) and total area (T)

Herbage mass	/Animal sp.	Net production (np) kg DM ha^{-1} day^{-1}		Total consumption (c) kg OM ha^{-1} day^{-1}		Balance (c/np)	
		Tnp	Gnp	Tc	Gc	G	T
1600	C	53.6	34.4	48.0	63.0	1.84	0.9
	S	55.9	44.2	33.0	46.5	1.05	0.6
	C+S	53.8	45.2	43.3	58.5	1.30	0.8
1900	C	48.7	60.2	30.6	45.0	0.75	0.6
	S	87.3	59.2	26.0	51.0	0.86	0.3
	C+S	82.3	88.6	37.0	61.7	0.70	0.5

(Growth-Senescence) at the low herbage mass but not at the high (Table D4.4). Net herbage accumulation rate (Growth-Senescence-Consumption) at the 1900 mass was as high as the measured rate of total herbage consumption, and so the assumption of steady state is only partially supported by the results. However it may be argued that since there was a proportion of the total area that was only partially grazed, net herbage accumulation should not necessarily be zero. If the assumption is made that the animals were grazing only on the short areas, a reasonable balance can be shown between the rates of net herbage production and rate of herbage consumption (Table D4.4). The grazing efficiencies shown in Table D4.4 indicate that the herbage mass on short areas was slightly decreasing at the 1600 and slightly increasing at the 1900 mass whilst the tall areas were possibly increasing in mass in both treatments. However, estimates of net herbage accumulation over the measurement period were not accurate enough to substantiate these suggestions. This illustrates the difficulty of making accurate estimates of net sward change over short periods of time. Since the assumption that animals grazed only the areas covered by short vegetation is not completely valid, some sort of intermediate equilibrium may have occurred in reality. Bircham (1981b) makes the point that steady state in one parameter does not necessarily mean that other parameters of the sward may be regarded as being constant. The results from this experiment also suggest that, although steady state may be maintained in some areas of the sward it does not mean that the whole area is under the same equilibrium.

The concept of steady state in grazed swards should be treated

with caution when interpreting experimental results.

Animal Measurements

Organic matter intake

In Experiment 3 cattle appeared to be more sensitive than sheep to changes in herbage mass, as shown by a greater reduction in the rate of intake between intermediate and low herbage mass. In the present experiment both species showed similar responses to changes in herbage mass. These results may be largely explained by the different range of herbage mass maintained in the current experiment. The organic matter intake for wethers and yearling steers was in the same range as those measured for dry ewes and yearling heifers in Period 3 of Experiment 3. The rate of intake increased with herbage mass in cattle and sheep grazing alone and in combination (Table E4.13). The rate of intake of both species grazing in combination at the 1900 mass tended to be higher than the intake of the single species grazing at the same herbage mass. This result may have been the consequence of different grazing pressures on the mix-stocked treatments (Connolly and Nolan, 1976). However differences in grazing pressure should have been reflected in an increased herbage mass on the mix-stocked swards at the 1900 mass. Although herbage mass tended to be higher in this treatment the differences were not big enough to justify the higher rate of intake. Bond *et al* (1967) have suggested that social relationships developed under combined cattle and sheep grazing may affect animal performance by changes produced in the ingestive behaviour. However neither the magnitude nor the direction of the likely changes in grazing

behaviour or animal performance have ever been indicated. In the current experiment no particular pattern of association between both grazing species has been detected (Munuo, personal communication).

Botanical Composition and Digestibility of the Diet

The proportion of lamina increased, and the proportions of stem and dead tissue decreased, in both cattle and sheep grazing alone and in combination, as the herbage mass increased (Table E4.15). The proportion of lamina tended to be lower in the extrusa samples selected by cattle, and both species selected diets with lower lamina contents when grazing in combination than when grazing alone. The effect of a companion grazer was more marked at the lower herbage mass when competition for food was presumably higher. The interaction herbage mass x companion species however, was significant for sheep but not for cattle. This result suggests that although sheep were able to select diets with higher proportions of lamina, they were more sensitive than cattle to the competitive species. Higher lamina proportion in diets selected by sheep than in those selected by cattle when grazing in combination have been reported elsewhere (Dudzinski and Arnold, 1973; Hodgson and Grant, 1981; Forbes, 1982). However, single species grazing has never been included as a control comparison. From single species comparisons in Experiment 3 it was concluded that sheep might have some competitive advantages when grazing in combination, for lamina proportion and digestibility were higher and more stable when herbage mass changed. Similar conclusions may be drawn if comparisons between both

species are made when grazing singly or in combination, since in both cases the lamina proportion was lower in diets selected by cattle. However, neither the difference between species nor the modification in diet composition of a particular species by the presence of the other necessarily means that cattle and sheep have different food niches. Estimates of diet overlap index (Morisita *et al*, 1959; Horn, 1966) (Table E4.16) showed complete overlap between the composition of diets selected by cattle or sheep grazing alone or in combination, indicating that the two species selected similar diets. Apparently any likely differences in selection strategy were not evident because either animal husbandry (Schwartz and Ellis, 1981) or low diversity in the sward prevented them being expressed.

The differences in botanical composition were reflected on diet quality (Table E4.12) and this result is in line with other published evidence (Dudzinski and Arnold, 1973; Langlands and Sanson, 1976; Jamieson and Hodgson, 1979). However, these differences were too small to explain differences in animal production (see Table E4.12). This result confirms the view that little agricultural significance can be attached to the minor differences in the diet selected by both species in intensively grazed swards (Hodgson and Forbes, 1980).

CHAPTER 6

GENERAL DISCUSSION

Changes in herbage mass are generally used as a base of measurement for nearly all assessments of vegetation response to management (L't Mannetje, 1978). This includes the assessment of the effects of management practices such as fertiliser inputs, stocking rate, grazing methods or animal species on the net accumulation of the vegetation. Hodgson and Maxwell (1981) made the point that a better understanding of the grazing system function may be achieved if studies of fluxes of plant tissue are complemented with studies on both plant and animal populations. In the two field experiments carried out in the current project, herbage mass or sward surface height were maintained constant between animal species comparisons. However, both cattle and sheep created swards with different plant population dynamics (see pages 136 and 218) and this in turn was reflected in differences in the rates of tissue flow. This suggests that there may be some limitations to understanding the way in which grazing systems work when vegetation is only considered as a bulk of amorphous mass. However, this is not to suggest that herbage mass or sward surface height should be excluded from grazing experiments and replaced by studies on population dynamics.

Studies of tiller population dynamics are necessary to explain differences in tiller densities which in turn will explain the differences in tissue turnover rates. The balance between the rate of herbage consumption and the rate of net herbage production will in turn determine changes in herbage mass and sward surface height, and these two parameters were used to make management decisions. It may be argued that, because of

compensatory changes in tiller population density and weight of the survivor tillers (White and Harper, 1970; Hodgson *et al*, 1981), herbage mass and tiller density are usually related and the levels in one variable are determined by the levels in the other variable. However, in the two field experiments the weight per individual tiller and herbage mass were similar between animal species whilst total tiller populations were not. This suggests that the distribution of tiller size in the population grazed by different animal species may have been different. The distribution of tiller size in ungrazed herbaceous populations is skewed towards many smaller and fewer bigger individuals than the average of the population (Obeid, Machin and Harper, 1967; Naylor, 1975). The suggestion made in Experiment 2 that grazing might tend to normalise this distribution, based on the higher chance of the taller tillers being defoliated by grazing sheep (Hodgson and Ollerenshaw, 1969; McIvor and Watkin, 1973), may need to be re-examined.

Under cattle grazing there may be two sources of modification of the distribution of size of plant population. Tallest tillers may still have the higher chance of being defoliated and thus of being reduced in size, but uprooted tillers which disappear from the plant community may generally be of relatively small size. Tallowin (1981) showed that a wide spectrum in tiller age classes may be expected under continuous cattle-stocking, but no size classification in either cattle- or sheep-grazed swards have ever been described.

The differential characteristics that both animal species appeared to impress on the grazed sward, i.e. higher tiller number and net herbage production in sheep-grazed swards, confirmed in

some degree similar descriptions reported elsewhere (Mitchell and Glenday, 1958 ; Boswell, 1978; Monteath *et al*, 1977; Boswell and Crawford, 1978; Boswell and Cranshaw, 1978; Briseno de la Hoz, 1981). However, the results reported by Joyce (1970) suggest that there may be some other uncontrolled conditions that might reverse these characteristics. Nevertheless, the fact that different swards are created by different animal species gives support to the view by Holmes (1976) that it is necessary to distinguish between swards suitable for sheep and swards suitable for cattle. However, the effects of a combination of cattle and sheep seem unlikely to lie outside the range delineated by the species singly. Thus tiller population densities under mixed-stocking may resemble populations created by the species in the highest numerical proportion in a mixed animal population.

Perennial ryegrass seems to be a well adapted sward species for sheep grazing systems, at least in the British Isles, but ryegrass tillers were regularly uprooted by grazing cattle. Monteath *et al* (1977) and Boswell and Crawford (1978), both suggested that cocksfoot was a better adapted plant species for cattle grazing than ryegrass. The argument was that, at least under Invermay conditions in central S. New Zealand, cocksfoot populations appeared to be more stable than ryegrass populations grazed by cattle. These authors attributed the greater loss to uprooting of ryegrass tillers to the greater tensile strength of their leaves, and thus their greater resistence to breaking in the pulling action characteristic of the harvesting mechanism developed by cattle (Arnold and Dudzinski, 1978). On the other hand, uprooting may be expected to be lower in plant species with

a lower leaf tensile strength (Monteath *et al*, 1977). The variability of tensile strength within and between species (Evans, 1964, 1967a, b) suggests that it may be possible to find alternative genotypes or species less sensitive to uprooting than the variety of perennial ryegrass used in the current studies.

The importance of maintaining high tiller densities in grazed swards as a means of controlling the amplitude of the fluctuation in herbage production within and between years has been emphasised by Hodgson and Wade (1978). The effect of tiller density on short term instability in the rate of net herbage production may be clearly illustrated by the differences in tissue turnover observed in both field experiments. The long term effects were suggested by the changes in the relative population densities of the component species of the plant populations over winter (see Tables A3.6 and A4.8). Changes in the relative proportions of the components of the total population may introduce instability in the rate of net herbage production if the invader species are less productive than those originally sown.

From the experiments described here cattle swards appeared to be more unstable than sheep swards, both within and between seasons, and tiller numbers in cattle grazed swards were relatively sensitive to changes in herbage mass. However, differences in tiller density established in swards grazed by cattle and sheep can be reversed by switching the animals between paddocks (Boswell and Crawford, 1978). Similar effects may be expected if part of the cattle population is replaced by an equivalent sheep

population. Densities in swards grazed by cattle and sheep in combination appeared to be similar to these on sheep-grazed swards, but they may become more similar to densities under cattle grazing if the relative proportions of cattle increases in mixed animal populations.

Grazing cattle and sheep in combination will improve the efficiency of utilisation of herbage if the selection of grazing site (Milne *et al*, 1979) and/or selection of individual plants (Hodgson, 1982 .) are complementary between species. From both field experiments it appeared that the between-animal species differences in grazing efficiency were rather seasonal and that they were overridden by grazing pressure effects. Both cattle and sheep grazing alone left similar proportions of under-grazed areas (see Tables E3.7 and E4.1). However, variability in sward surface height was higher in cattle paddocks than in sheep paddocks, particularly at low grazing pressure because of the greater accumulation of herbage on tall areas. The effect of combining animal species was apparently reflected in a reduction in the variance of sward surface height compared with the variance in cattle grazed swards. This may be due to the reduced stocking rate of cattle under mixed species grazing and the consequent reduction in the area affected by cattle dung, or to a reduction in herbage mass on areas affected by cattle dung as a consequence of some grazing by sheep (Nolan, 1980). The evidence from the two field experiments does not make it possible to determine the relative importance of these two effects. The visual impression in Experiment 4 was that the ungrazed areas were less prominent

on mixed plots than on cattle grazed plots (Plate E4.2) but in that experiment herbage mass on ungrazed areas did not differ significantly between animal species. Furthermore the proportion of the total area left ungrazed at any time was similar under single-species and mixed-species grazing, and did not differ materially between cattle and sheep (see Table E4.1).

Bite selection may be associated with the frequency that a particular plant species is found in the diet selected by different animal species. Animal species with different food niches are expected to use the vegetation more efficiently when grazing in combination than when grazing alone. Differences of 0.1-0.15 in the frequency that a particular morphological part of a plant or plant species occurred in diets selected by cattle and sheep were found in both experiments, and bigger differences have been reported elsewhere (Dudzinski and Arnold, 1973). The diets selected by both species showed high overlap (see Tables E3.19 and E4.16) as expressed by the index suggested by Morisita (1958) and Horn (1969), indicating that the two animal species selected virtually identical diets. However, sheep and cattle grazing natural hill communities at a very low grazing pressure (Grant and Hodgson, 1980) showed marked differences in the components selected, overlap indices ranging between 0.46 and 0.61. This is clear evidence of complementary bite selection under these conditions.

Schwartz and Ellis (1981) concluded that sheep husbandry has prevented the expression of the theoretical selective advantages developed under natural selection. The comparison

of the results of the current experiments with those reported by Grant and Hodgson (1980) would suggest that grazing management may also limit the expression of differences in selective behaviour which are otherwise characteristic of sheep and cattle. The fact that both species, when grazing in combination selected diets with a lower lamina proportion than when grazing alone (see Table E4.15) suggests that, under intensive management, competitive rather than complementary use of the vegetation may be expected.

Under intensive grazing management an increase in herbage growth rate should be reflected in a higher rate of intake per animal, so long as animal numbers are kept constant (Hodgson and Forbes, 1980). In both field experiments increased growth rates were cancelled out by increasing stocking rate. However, in both species the individual rate of intake was modified when herbage mass changed. Under the more extreme conditions of Experiment 3 sheep were better able to maintain intake at low herbage mass than cattle. When both species grazed in combination at low grazing pressure, sheep had the highest rate of intake per unit of live weight.

The results of this study suggest that there is little reason to expect that net herbage production will be higher under mixed grazing than under grazing by either sheep or cattle alone. At similar grazing pressures cattle-grazed swards would be expected to have lower tiller densities than sheep-grazed swards and this in turn will result in a depression in net herbage production. However, the addition of sheep to a cattle-grazing system should result in the maintenance of tiller density and consequently net herbage production at levels close to those

expected from sheep-grazed swards. When swards are intensively grazed mixed stocking does not appear to result in a greater efficiency of herbage utilisation than is achieved by either sheep or cattle grazing alone. The evidence demonstrated almost complete overlap in the diets selected by sheep and cattle. There is therefore no reason to expect that mixed species grazing management will result in synergistic effects upon herbage production and utilisation, though there is evidence of the existence of competitive advantages to sheep in the maintenance of herbage intake under limiting sward conditions.

In this study attention was concentrated principally upon the reaction of the sward to variations in grazing management. It must be concluded that the production advantages to mixed stocking management which have been demonstrated in some studies (see Nolan and Connolly, 1977 and Hamilton, 1980) are not attributable to advantages in those aspects of the grazing systems affecting herbage production and utilisation.

REFERENCES

ALEXANDER, R.H. and McGOWAN, Mary 1966. The routine determination of *in vitro* digestibility of organic matter in forages. An investigation of the problems associated with continuous large-scale operation. Journal of the British Grassland Society, *21*, 140-147.

ALLDEN, W.G. 1962. Rate of herbage intake and grazing time in relation to herbage availability. Proceedings of the Australian Society of Animal Production, *4*, 163.

ALLISON, R.M. 1963. Phasic growth of the leaves of cereal. Nature, *198*, 809-810.

ANSLOW, R.C. and GREEN, J.O. 1967. The seasonal growth of pasture grasses. Journal of Agricultural Science, Cambridge, *68*, 109-122.

A.R.C. 1980. The nutrient requirements of ruminant livestock. Agricultural Research Council Working Party. Commonwealth Agricultural Bureaux, Slough, England.

ARMITAGE, P. 1971. Statistical Methods in Medical Research. Oxford: Blackwell Scientific Publications 504 pp.

ARNOLD, G.W. and DUDZINSKI, M.L. 1978. Ethology of free ranging domestic animals. Elsevier Scientific Publishing Company, Oxford.

ATTWOOD, E.A. and HEAVEY, J.F. 1964. Determination of grazing livestock units. Irish Journal of Agricultural Research *3*, 249-251.

BAKER, R.D. 1964. Grassland recording. III A reappraisal of the use of livestock and starch-equivalent standards in assessing the utilised production from grassland. Journal British Grassland Society, *19*, 149-155.

BAKER, R.J. and NELDER, J.A. 1978. General Linear Interactive Modelling. Numerical Algorithms Group, Oxford, England.

BARROW, N.J. 1967. Some aspects of the effects of grazing on the nutrition of pastures. Journal of the Australian Institute of Agricultural Science, *3*, 254-262.

BARTHRAM, G.T. 1980. Sward structure and the depth of the grazed horizon. Proceedings of the British Grassland Society Winter Meeting 1980. Grass and Forage Science, *36*, 130-131.

BEAN, E.W. 1964. The Influence of Light Intensity upon the Growth of an S37 Cocksfoot (*Dactylis glomerata*) Sward. Annals of Botany, N.S. *28*,427-443.

BEGG, J.E. and WRIGHT, M.J. 1962. Growth and development of leaves from intercalary meristems in *Phalaris arundinacea* L. Nature,*194*,1097-1098.

BELL, R.H.V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. In: Animal Populations in Relation to their Food Reserves. Ed. by Watson, A. Symposium British Ecological Society 1970.

BERNARD, J.M. 1976. The Life History and Population Dynamics of Shoots of *Carex rostrata*. Journal of Ecology,*64*,1045-1048.

BIRCHAM, J.S. 1980. Herbage mass and height: their relevance to management systems. Proceedings of Workshop on Mixed Grazing. The Agricultural Research Institute, Ireland and The Agricultural Research Institute, Iceland, 93-98.

BIRCHAM, J.S. 1981a. The effects of a change in the herbage mass on herbage growth, senescence and net production rates in continuously stocked mixed species sward. In: C.E. Wright (ed). Plant Physiology and Herbage Production, British Grassland Society Occasional Symposium, Nottingham, 85-87.

BIRCHAM, J.S. 1981b. Herbage growth and utilisation under continuous stocking management. Ph.D. Thesis, University of Edinburgh.

BIRCHAM, J.S. and HODGSON, J. 1981. The dynamics of herbage growth and senescence in a mixed species temperate sward continuously grazed by sheep. In: Proceedings of the XIV International Grassland Congress, Lexington, U.S.A. In press.

BLACK, W.J.M. 1980. Integrated beef and sheep grazing. In: Proceedings of Workshop on Mixed Grazing. The Agricultural Research Institute, Ireland. The Agricultural Research Institute, Iceland, 68-81.

BOND, J., CARLSON, G.E., JACKSON, C. and CURRIE, W.A. 1967. Social cohesion of steers and sheep as a possible variable in grazing studies. Journal of Agronomy, *59*, 481-483.

BOSWELL, C.C. 1978. Comparisons of cattle grazing and sheep grazing. Proceedings of New Zealand Grassland Association *38*, part 1, 56-65.

BOSWELL, C.C. and CRANSHAW, L.J. 1978. Mixed grazing of cattle and sheep. Proceedings of New Zealand Society of Animal Production, *38*, 116-120.

BOSWELL, C.C. and CRAWFORD, A.J.M. 1978. Changes in the perennial ryegrass component of grazed pastures. Proceedings of New Zealand Grassland Association, *40*, 125-135.

BOYER, J.S. 1970. Leaf enlargement and metabolic rates in corn, soybean, and sunflower at various leaf water potentials. Plant Physiology, *46*, 233-235.

BRELIN, B. 1979. Mixed grazing with sheep and cattle compared with simple grazing. Swedish Journal of Agricultural Research, *9*, 113-120.

BRISENO DE LA HOZ, V.M. and WILMAN, D. 1981. Effects of cattle grazing, sheep grazing, cutting and sward height on grass-white clover sward. Journal of Agricultural Science, Cambridge, *97*, 699-706.

BROCKINGTON, N.R. 1972. A mathematical model of pasture contamination by grazing cattle and the effects on herbage. Journal of Agricultural Science Cambridge, *79*, 249-257.

BROUGHAM, R.W. 1958. Leaf development in swards of white clover *(Trifolium repens* L.) New Zealand Journal of Agricultural Research, *1*, 707-718.

BROUGHAM, R.W. 1959. The effects of frequency and intensity of grazing on the productivity of a pasture of short rotation ryegrass and red and white clover. New Zealand Journal of Agricultural Research, *2*, 1232-1247.

BROWN, R.K. and EVANS, P.S. 1973. Animal Treading - A review of the work of the late D.B. Edmond, New Zealand Journal of Experimental Agriculture, *1*, 217-226.

CALLAGHAN, T.V. 1976. Growth and population dynamics of *Carex bigelowie* in an Alpine environment. Strategies of growth and population dynamics of tundra plants 3. Oikos, *27*, 402-413.

CLARK, K.W. 1963. Stocking rate and sheep:cattle interactions. Wool Technology and Sheep Breeding, *10*, 27-32.

COCHRAN, W.G. and COX, G.M. 1956. Experimental Designs. New York. J. Wiley and Sons, Inc. Chapman and Hall Limited London, p. 454.

COCKAYNE, L. (1926). Tussock grassland investigation in New Zealand. In: Aims and Methods in the Study of Vegetation. Eds. A.G. Tansley and T.T. Clipp, London, Crown Agents for the Colonies, pp. 349-72.

CONNIFFE, D. 1976. A comparison of between and within herd variance in grazing experiments. Irish Journal of Agricultural Research, *15*, , 39-46.

CONNOLLY, J. and NOLAN, T. 1976. Design and analysis of mixed grazing experiments. Animal Production, *23*, 63-71.

CONNOLLY, J. 1980. Some experimental and statistical methods and problems in competition studies. Proceedings of Workshop on Mixed Grazing. The Agricultural Research Institute, Ireland. The Agricultural Research Institute, Iceland, 164-182.

CONWAY, A.G. 1973. Voluntary intake and stocking rate equivalents for grazing cattle. Irish Journal of Agricultural Research *12*, 193-204.

CONWAY, A., McLOUGHLIN, A. and MURPHY, W.E. 1972. Development of a cattle and sheep farm. Animal management series No. 2. An Foras Taluntais, Dublin.

COOPER, J.P. 1951. Studies on growth and development in *Lolium*. II. Pattern of bud development of the shoot apex and its ecological significance. Journal of Ecology, *29*, 228-270.

CORBETT, J.L., GREENHALGH, J.F.D. and McDONALD, A.P. 1958. Paper as a carrier of chromium sesquioxide. Nature, London *182*, 1014-1016.

CORNISH, E.A. 1936. Non-replicated factoral experiments. Journal Australian Institute of Agricultural Research, *2*, 79-82.

DAVIES, A. 1974. Leaf tissue remaining after cutting and regrowth in perennial ryegrass. Journal of Agricultural Science, Cambridge, *82*, 165-172.

DAVIES, A. 1977. Structure of the grass swards. Proceedings of International Meeting of Animal Production from Temperate Grassland. In Grass and Agricultural Society, An Foras Taluntais, 36-44.

DAVIES, A. 1981. Tissue turnover in the sward. In Sward Measurement Handbook. Ed. J. Hodgson, R.D. Baker, A. Davies, A.S. Laidlaw, J.D. Leaver, British Grassland Society, 179-208.

DAVIDSON, J.L. 1969. Growth of grazed plants. Proceedings of the Australian Grasslands Conference *2*, 125-137.

DAVIDSON, J.L. and MILTHORPE, F.L. 1966. Leaf growth in *Dactylis glomerata* following defoliation. Annals of Botany, N.S. Vol. *30*, 173-184.

DAVIDSON, J.L. and ROBSON, M.J. 1981. Photosynthesis, leaf age and canopy structure in a mixed clover/ryegrass sward. Grassland Research Institute Annual Report, Hurley, 1980.

DE LUCIA SILVA, R.G. 1974. A study of the variation in the defoliation and regrowth of individual tillers in swards of *Lolium perenne* L. grazed by sheep. A Thesis towards the degree of Doctor of Philosophy. University of Reading.

DENNIS, W.D. and WOLEDGE, Jane 1981. The photosynthesis of white clover leaves in a mixed clover/ryegrass sward. In: C.G. Wright (ed). Plant Physiology and Herbage Production, British Grassland Society Occasional Symposium, Nottingham, 191-192.

DENNIS, W.D. and WOLEDGE, Jane 1982. Photosynthesis by white clover leaves in mixed clover/ryegrass swards. Annals of Botany, *49*, 627-635.

DUDZINSKI, M.L. and ARNOLD, G.W. 1973. Comparison of diets of sheep and cattle grazing together on sown pastures on the Southern tablelands of New South Wales by principal components analysis. Australian Journal of Agricultural Research, *24*, 899-912.

EADIE, J. 1981. Production systems in the hills and uplands: a critical assessment of current thinking. In: Efficient Use of Forage and Animal Resources in the Hills and Uplands. Ed. J. Frame, British Grassland Society Occasional Symposium, No. 12, 95-103.

EDMOND, D.B. 1958. The influence of treading on pasture, a preliminary study. New Zealand Journal of Agricultural Research, *1*, 319-328.

EDMOND, D.B. 1964. Some effects of sheep treading on the growth of 10 pasture species. New Zealand Journal of Agricultural Research, 7, 1-16.

EDMOND, D.B. 1966. The influence of animal treading on pasture growth. Proceedings of the X International Grassland Congress, 453-458.

EDMOND, D.B. 1970. Effects of treading on pasture, using different animals and soils. Proceedings of XI International Grassland Congress, 604-608.

EVANS, P.S. 1964. A study of leaf strength in four ryegrass varieties. New Zealand Journal of Agricultural Research, 7, 508-513.

EVANS, P.S. 1967a. Leaf strength studies of pasture grasses. I. Apparatus techniques and some factors affecting leaf strength. Journal of Agricultural Science, Cambridge, *69*, 171-174.

EVANS, P.S. 1967b. Leaf strength studies of pasture grasses. II. Strength cellulose content and sclerenquima tissue proportions of eight grasses grown as single plant. Journal of Agricultural Science, Cambridge, *69*, 175-181.

EVANS, P.S. 1973. Effect of seed size and defoliation at full developmental stages on root and shoot growth of seedling of some common pasture species. New Zealand Journal of Agricultural Research, *16*, 389-394.

FENLON, J.S. 1978. Defoliation frequency on set stocked swards. Annual Report of the Grassland Research Institute, 1978, 101-102.

FORBES, T.D.A. 1982. Ingestive behaviour and diet selection in grazing cattle and sheep. Ph.D. Thesis, University of Edinburgh.

FRAME, J. 1976. A comparison of herbage production under cutting and grazing (Including comments on deleterious factors such as treading). Proceedings of the 8th Occasional Symposium of the British Grassland Society, 39-49.

GIBB, M.J., TREACHER, T.T. and JOICEY, S.A. 1972. A case of rejection by lambs of regrowths from previously grazed ryegrass swards. Proceedings British Society of Animal Production, 1972, *178*.

GIFFORD, R.M. and MARSHALL, C. 1973. Photosynthesis and assimilate distribution in *Lolium* and *Trifolium* Lam. following differential defoliation. Australian Journal of Biological Science *26*, 517-526.

GRAHAM, N. McC. 1972. Units of metabolic body size for comparisons amongst adult sheep and cattle. Proceedings of the Australian Society of Animal Production, *9*, 352-355.

GRANT, Sheila A. 1981. Sward components. In: Hodgson, J., Baker, R.D., Davies, Alison, Laidlaw, A.S. and Leaver, J.D. (eds). Sward Measurement Handbook, British Grassland Society, Hurley, pp 71-92.

GRANT, S.A., BARTHRAM, G.T. and TORVELL, L. 1981a. Components of regrowth in grazed and cut *Lolium perenne* swards. Grass and Forage Science, *36*, 155-168.

GRANT, S.A. and HODGSON, J. 1980. Comparative studies of diet composition and herbage intake by sheep and cattle grazing a range of native hill pastures. Proceedings of 8th General Meeting European Grassland Federation, *5*, 39-47.

GRANT, S.A., KING, J., BARTHRAM, G.T. and TORVELL, L. 1981b. Responses of tiller population to variation in grazing managements in continuously stocked swards as affected by time of year. In: C.G. Wright (ed) Plant Physiology and Herbage Production. British Grassland Society Occasional Symposium Nottingham, 81-84.

GREENHALGH, J.F.D. and REID, G.W. 1969. The effects of grazing intensity on herbage consumption and animal production. III. Dairy cows grazed at two intensities on clear or contaminated pastures. Journal of Agricultural Science, Cambridge, *72*, 223-228.

GRIME, J.P. 1974. Vegetation classification by reference to strategies. Nature, London, *250*, 26-31.

HAMILTON, D. 1980. Effects of mixed stocking of sheep and cattle in Australia. I. Effects on animal performance and diet selection. Proceedings of the workshop on mixed grazing. Galway Agricultural Institute of Ireland and Agricultural Institute of Iceland.

HARPER, J.L. 1967. A Darwinian approach to plant ecology. Journal of Ecology, *55*, 247-270.

HARPER, J.L. 1970. Grazing, fertilisers and pesticides in the management of grasslands. The Scientific Management of Animal and Plant Communities for Conservation. Ed. by E. Duffen and Watt, H.S. pp. 15-31.

HARPER, J.L. 1977. Population biology of plants. (Academic Press : London).

HEADY, H.F. and TORELL, D.T. 1959. Forage preference exhibited by sheep with oesophageal fistulas. Journal of Range Management Volume *12*, pp. 28-37.

HILDER, H.J. 1966. The distribution of plant nutrients by sheep at pasture. Proceedings of the 10th International Grassland Congress, Helsinki, 977-981.

HILL, M.J. and WATKIN, B.R. 1975. Seed production studies on perennial ryegrass, timothy and prairie grass. 1. Effect of tiller age on tiller survival, ear emergence and seed head components. Journal of the British Grassland Society, *30*, 63-71.

HODGSON, J. 1966. The frequency of defoliation of individual tillers in a set-stocked sward. Journal of the British Grassland Society, *21*, 258-263.

HODGSON, J. 1974. The effect of the grazing animal on herbage quality and utilisation. Proceedings of 5th General Meeting, European Grassland Congress, Uppsala 1973, Vaxtolling, *28*, 74-80.

HODGSON, J. 1976. The influence of grazing pressure and stocking rate on herbage intake and animal performance. In: Pasture Utilisation by the Grazing Animal. British Grassland Society, Occasional Symposium, *8*, 93-103.

HODGSON, J. 1979. Nomenclature and definitions in grazing studies. Grass and Forage Science, *34*, 11-18.

HODGSON, J. 1977. Factors limiting herbage intake by the grazing animal. Proceedings of International Meeting, Animal Production from Temperate Grassland. Irish Grassland and Animal Production Association, Dublin 1977.

HODGSON, J. 1981a. Sward studies: objectives and priorities. In: Sward Measurement Handbook. J. Hodgson, R.D. Baker, A. Davies, A.S. Laidlaw, J.D. Leaver (ed), 1-14.

HODGSON, J. 1981b. Variations in the surface characteristics of the sward and the short-term of herbage intake by calves and lambs. Grass and Forage Science, *36*, 49-57.

HODGSON, J. 1982. Influence of sward characteristics on diet selection and herbage intake by the grazing animal. Proceedings of International Symposium on Nutritional Limits to Production from Forage. Brisbane 1981, 153-166.

HODGSON, J., BIRCHAM, J.S., GRANT, S.A. and KING, J. 1981. The influence of cutting and grazing management on herbage growth and utilisation. In: Plant Physiology and Herbage Production. Ed. C.E. Wright. British Grassland Society Occasional Symposium No. 13, 51-62.

HODGSON, J. and FORBES, T.D.A. 1980. Mixed grazing : herbage growth and grazing efficiency. In: Proceedings Workshop on Mixed Grazing. Galway, September 1980, *81*, 88.

HODGSON, J. and GRANT, S.A. 1981. Grazing animals and forage resources in the hills and uplands. In: Frame, J. (ed). Forage and Animal Resources in the Hills and Uplands. Proceedings of a British Grassland Society Symposium Edinburgh 1980.

HODGSON, J. and MAXWELL, T.J. 1981. Grazing research and grazing management. The Hill Farming Research Organisation Biennial Report, 169-187.

HODGSON, J. and OLLERENSHAW, J.H. 1969. The frequency and severity of defoliation of individual tillers in set-stocked swards. Journal British Grassland Society, *24*, 226-234.

HODGSON, J. and RODRIGUEZ CAPRILES, J.M. 1970. The measurement of herbage intake in grazing studies. Annual Report of the Grassland Research Institute, 1970, pp. 132-140.

HODGSON, J. and WADE, M.H. 1978. Grazing management and herbage production. Proceedings British Grassland Society Winter Meeting 1978. Grazing Sward Production and Livestock Output.

HOLMES, W. 1976. Summing up. In: Pasture Utilisation by the Grazing Animal. Ed. Hodgson J. and Jackson, D.K. Occasional Symposium No. 8, British Grassland Society.

HOPKINSON, J.M. 1966. Studies on the expansion of the leaf surface. VI. Senescence and the usefulness of old leaves, Journal of Experimental Botany, *17*, 762-770.

HORN, H.S. 1966. Measurement of 'Overlap' in comparative ecological studies. American Naturalist, *100*, 419-424.

JACKSON, D.K. 1976. The influence of patterns of defoliation on sward morphology. In: Pasture Utilisation by the Grazing Animal. Ed. Hodgson, J. and Jackson, D.K. Occasional Symposium No. 8. British Grassland Society, pp 51-60.

JAMIESON, W.S. and HODGSON, J. 1979. The effects of variation in sward characteristics upon the ingestive behaviour and herbage intake of calves and lambs under a continuous stocking management. Grass and Forage Science, *34*, 273-282.

JONES, M.G. 1933a. Grassland management and its influence on the sward. Part I. Factors influencing the growth of pasture plants. The Empire Journal of Experimental Agriculture, *1*, 43-57.

JONES, M.G. 1933b. Grassland management and its influence on the sward. Part II. The management of a clover sward and its effects. The Empire Journal of Experimental Agriculture, *1*, 123-128.

JONES, M.G. 1933c. Grassland management and its influence on the sward. Part III. The management of a 'grassy' sward and its effects. The Empire Journal of Experimental Agriculture, *1*, 223-234.

JONES, M.G. 1933d. Grassland management and its influence on the sward. Part IV, The management of poor pastures. Part V. Edaphic and biotic influences on pastures. The Empire Journal of Agricultural Research, *1*, 361-367.

JONES, R.M. and MOTT, J.J. 1980. Population dynamics in grazed pastures. Tropical Grasslands, *14, No. 3*, 218-224.

JOYCE, J.P. 1970. Intensive beef and sheep production. Proceedings of the New Zealand Grassland Association, 168-180.

KAYS, S. and HARPER, J.L. 1974. The regulation of plant and tiller density in the grass sward. Journal of Ecology *62*, 97-105.

KYDD, D.D. 1964. The effect of different systems of cattle grazing on the botanical composition of permanent lowland pasture. Journal of Ecology, *52*, 139-149.

KYDD, D.D. 1966. The effect of intensive sheep stocking over a five year period on the development and production of the sward. Journal of the British Grassland Society, *21*, 284-298.

LANGER, R.H.M. 1954. A study of leaf growth in Timothy *Phleum pratense*. Journal of the British Grassland Society, *9*, 275-284.

LANGER, R.H.M. 1959. Growth and nutrition of Timothy *Phleum pratense*. 5. Growth and flowering at different levels of nitrogen. Annals of Applied Biology *47*, 740-751.

LANGER, R.H.M. 1963. Tillering in herbage grasses. Herbage Abstract *33*, 141-147.

LANGER, R.H.M. 1979. How Grasses Grow. Studies in Biology *34*, 2nd edition, Edward Arnold Limited, London.

LANGER, R.H.M., RYLE, S.M. and JEWIS, O.R. 1964. The changing plant and tiller, populations of Timothy and Meadow Fescue swards. I. plant survival and pattern of tillering. Journal of Applied Ecology *1*, 197-208.

LANGLANDS, J.P. and SANSON, J. 1976. Factors affecting the Nutritive Value of the Diet Composition of Rumen Fluid of Grazing Sheep and Cattle. Australian Journal of Agricultural Research, *27*, 691-707.

LEAFE, E.L., STILES, W. and JONES, M.B. 1975. The physiology of the sward in the field. Annual Report of the Grassland Research Institute, Hurley, 1974, 39-41.

LEIGH, J.H. 1974. Diet selection and effects of grazing on the composition and structure of semiarid vegetation. In Studies of the Australian arid zone, Vol.2. Animal Production, ed. A.D. Wilson, 102-126. CSIRO, Melbourne, Australia.

LEOPOLD, A.C. 1980. Ageing and Senescence in Plant Development. In Senescence in Plants. Ed. Thimann, K.V. CRC Press Boca Raton Florida. pp. 2-11.

MACARTHUR, R.H. and LEVINS, R. 1967. The limiting similarity convergence and divergence of coexisting species. American Naturalist, *101*, 377-385.

McIVOR, P.J. and WATKIN, B.R. 1973. The pattern of defoliation of Cocksfoot by grazing sheep. Proceedings of the New Zealand Grassland Association, *34*, 225-235.

MANNETJE, L. 't. 1978. Measuring quantity of grassland vegetation. In Measurement of Grassland Vegetation and Animal Production. Ed. L. t'. Mannetje. Bulletin 52 CAB. pp 63-95.

MARSH, R. and CAMPLING, R.C. 1970. Fouling of pastures by dung. Herbage Abstract, *40*, 123-130.

MARSHALL, C. and SAGAR, G.R. 1965. The Influence of Defoliation on the Distribution of Assimilates in *Lolium multiflorum* Lam. Annals of Botany, N.S. *29*, 265-370.

MARSHALL, C. and SAGAR, G.R. 1968. The Interdependence of Tillers in *Lolium multiflorum* Lam. A quantitative assessment. Journal of Experimental Botany, *19*, 785-794.

MATTHEWS, C.P. and WESTLAKE, D.F. 1969. Estimation of production by a population of higher plants subject to high mortality. Oikos *20*, 156-160.

MILNE, J.A., BAGLEY, L., GRANT, S.A. 1979. Effects of season and level of grazing on the utilisation of heather by sheep. 2. Diet selection and intake by sheep. Grass and Forage Science *34*, 45-53.

MILNE, J.A., HODGSON, J., THOMPSON, R., SOUTER, W.G., and BARTHRAM G.T. 1982. The diet ingested by sheep grazing swards differing in white clover and perennial ryegrass content. Grass and Forage Science *37*, 209-218.

MITCHELL, K.J. and COLES, T.J. 1955. Effects of defoliation on shading on short rotation ryegrass. New Zealand Journal of Science and Technology, Series A *36*, 586-604.

MITCHELL, K.J. and GLENDAY, A.C. 1958. The tiller population of pastures. New Zealand Journal of Agricultural Research *3*, 305-318.

MONTEATH, M.A., JOHNSTONE, P.D. and BOSWELL, C.C. 1977. Effects of animals on pasture production. I. Pasture productivity from beef cattle and sheep farmlets. New Zealand Journal of Agricultural Research *20*, 23-30.

MORISITA, M. 1959. Measuring up of interspecific association and similarity between communities. Memoirs Faculty of Science, Kyushu University. Series E Biology *3*, 65-80.

MORLEY, F.H.W. 1978. Animal Production Studies on Grassland. In Measurement of the Grassland Vegetation and Animal Production. Ed. L. 't. Mannetje. Bulletin 52 CAB. pp 103-162.

MORLEY, F.H.W. 1981. Management Systems. In Grazing Animals. Ed. F.H.W. Morley, World Animal Science, B1, Elsevier Scientific Publishing Company, Amsterdan-Oxford-New York pp. 379-400.

MORLEY, F.H.W. and DONALD, A.D. 1980. Farm management and systems of helminth control. Veterinary Parasitology *6*, 105-134.

MORLEY, F.H.W. and SPEDDING, C.R.W. 1968. Agricultural Systems and Grazing Experiments. Herbage Abstracts *38*,279-287.

MORRIS, R.M. 1970. The use of cutting treatments designed to simulate defoliation by sheep. Journal of the British Grassland Society *25*, 198-206.

MULHOLLAND, J.G., COOMBE, J.B. and McMANUS, W.R. 1977. Diet selection and intake by sheep and cattle grazing together on stubbles of wheat, oats and barley. Australian Journal of Experimental Agriculture and Animal Husbandry *17*, 224-229.

N.A.G. 1980. GENSTAT reference manual. Numerical Algorithms Group, Oxford, England.

NAYLOR, R.E.L. 1976. Changes in the structure of plant populations. Journal of Applied Ecology *13*, 513-521.

NOLAN, T. 1977. An ecological appraisal of mixed grazing. Paper to 28th. Annual Meeting E.A.A.P., Brussels.

NOLAN, T. 1980. Research on mixed grazing by cattle and sheep in Ireland. Proceedings workshop on mixed grazing. Agricultural Institute of Ireland and Agricultural Institute of Iceland, Galway, 1980. pp 1-19.

NOLAN, T. and CONNOLLY, J. 1977. Mixed stocking by sheep and steers - a review. Herbage Abstracts *47*, 367-374.

NORMAN, M.J.T. 1957. The influence of various grazing treatments upon the botanical composition of a downland permanent pasture. Journal of the British Grassland Society *12*, 246-263.

NORMAN, M.J.T. and GREEN, J.O. 1958. The local influence of cattle dung and urine upon the yield and botanical composition of permanent pasture. Journal of the British Grassland Society *13*, 39-45.

OBEID, M., MACHIN, D. and HARPER, J.L. 1967. Influence of density on plant to plant variation in fibre flax *Linum Usitatissmun* L. Crop Science 7, 471.

ODUM, E.P. 1971. Fundamentals of Ecology. Therd edition W.B. Saunders Company, Philadelphia, London, Toronto.

ONG, C.K. 1978. The physiology of tiller death in grasses. 1. The influence of tiller age, size and position. Journal of the British Grassland Society *33*, 197-203.

ONG, C.K. and MARSHALL, G. 1979. The growth and survival of severely-shaded tillers in *Lolium perenne* L. Annals of Botany *43*, 147-155.

ONG, C.K., MARSHALL, C. and SAGAR, G.R. 1978. The physiology of the tiller death in grasses. 2. Cause of tiller death in a grass sward. Journal of the British Grassland Society *33*, 205-211.

PEACOCK, J.M. 1975a. Temperature and leaf growth in *Lolium perenne* L. I. The thermal microclimate: its measurement and relation to crop growth. Journal of Applied Ecology *12*, 99-117.

PEACOCK, J.M. 1975b. Temperature and leaf growth in *Lolium prenne* L. II. The site of temperature perception. Journal of Applied Ecology *12*, 115-123.

PEACOCK, M.J. 1975c. Temperature and leaf growth in *Lolium perenne* L. III. Factors affecting seasonal differences. Journal of Applied Ecology *12*, 685-697.

PEACOCK, J.M. 1976. Temperature and leaf growth in four grasses species. Journal of Applied Ecology *13*, 225-232.

PEART, J.N. 1963. Increased production from Hill Pastures, Sourhope Trials with cattle and sheep. Scotish Agriculture *42*, 147-151.

PINEIRO, J. and HARRIS, W. 1978. Performance of mixtures of ryegrass cultivars and prairie grass with red clover cultivars under two grazing frequencies. II. Shot populations and natural reseeding of prairie grass. New Zealand Journal of Agricultural Research *21*, 655-673.

PETERSEN, R.G., LUCAS, H.L., WOODHOUSE,. W.W. 1965. The distributiion of excreta by freely grazing cattle and its influences on pasture fertility. 1. Excretal density. Agronomy Journal *48*, 440-444.

REYNOLDS, P.L., BOND, J., CARLSON, G.E., JACKSON, C.H. jnr., HART, R.H.,LINDAHL, J.L. 1971. Co-grazing of sheep and cattle on an orchardgrass sward. Agronomy Journal *63*, 533-536.

ROBSON, M.J. 1973. The growth and development of simulated swards of perennial ryegrass. 1. Leaf growth and dry weight ghanges as selected for the ceiling yield of a seedling sward. Annals of Botany *37*, 487-500.

ROBSON, M.J. 1981. Potential Production. What is it and can we increase it ?. In Plant Physiology and Herbage Production Ed. C.E. Wright, British Grassland Society Occasional Symposium. pp 5-18.

ROBSON, M.J. and DEACON, M.J. 1978. Nitrogen deficiency in small closed communities of S24 ryegrass. II. Changes in the weight and chemical composition of single leaves during their growth and death. Annals of Botany *42*, 1199-1213.

ROBSON, M.J. and SHEEHY, J.E. 1981. Leaf area and light interception In Measurement Handbook. J. Hodgson, R.D. Baker, A. Davies A.S. Laidlaw, J.D. Leaver (ed). pp 115-139.

RYLE, G.J.A. 1970. Effects of two levels of applied nitrogen on the growth of S37 cockfoot in small simulated swards in a controlled environment. Journal of the British Grassland Society *25*, 40-49.

SCHWARTZ, C.H. and ELLIS, J.E. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the short grass prairie. Journal of Applied Ecology *18*,343-353.

SCOTT, R.S. 1977. Effects of animals on pasture production. II. Pasture production and N and K requirements of cattle and sheep pastures when measured under a common method of defoliation. New Zealand Journal of Agricultural Research *20*, 31-36.

SILSBURY, J.H. 1970. Leaf growth in pasture grasses. A review. Tropical Grasslands *4*, 17-36.

SCHUSTER, J.L. 1964. Root development of native plants under three grazing intensities. Ecology *45*, 63-70.

SMITH, A., ARNOTT, R.A. and MACAULLY, J.R. 1975a . Sward productivity underalternate or repeated cutting of adjacent small areas. Journal of the British Grassland Society *30*, 201-208

SMITH, A., ARNOTT, R.A. and PEACOCK, J.M. 1971b. A comparison of the growth of a cut sward with that of grazed swards, using a technique to eliminate fouling and treading. Journal of the British Grassland Society *26*,157-162.

SNAYDON, R.W. 1980. Plant Demography in Agricultural Systems. In Demography and Evolution in Plant Population. Botanical Monographs *15*, 131-160.

SNELL, M.G. 1935. Pasture gains of cattle and sheep. Proceedings of American Society of Animal Production, 1934. 142-144.

SPEDDING, C.R.W. 1971. Grassland Ecology. Clarendon Press, Oxford. 221p.

STOBBS, T.H. 1970. Automatic measurement of grazing time by dairy cows on tropical grass and legume pasture. Tropical Grassland *4*, 237-244.

SUKHATME, P.V. and SUKHATME, P.V. 1970. Sampling theory of surveys with application. Iowa State University Press, Iowa.

TAINTON, N.M. 1974. Effects of different grazing rotations of pasture production. Journal of the British Grassland Society *29*, 191-202.

TALLOWIN, J.R. 1981. The significance of tiller number changes under grazing. In Plant Physiology and Herbage Production. Ed. C.E. Wright. British Grassland Society Occasional Symposium *13*, 77-80.

THOMAS, H. 1977. The influence of autumn cutting regime on the response to temperature of leaf growth in perennial ryegrass. Journal of the British Grassland Society *23*, 227-230.

THOMAS, H. 1980. Terminology and definitions in studies of grassland plants. Grass and Forage Science *35*, 13-23.

TROUGHTON, A. 1955. Cessation of tillering in young grass plants. Nature *176*, 514.

VAN DYNE, G.M., BROCKINGTON, N.R., SZOCS, S., DUCK, J. and RIBIC, C.A. 1980. Large herbivore sub-system. In Grassland Systems Analysis and Man. Ed. A.I. Brymeyer and G.M Van Dyne, Cambrdge University Press, 269-537.

VAN KEUREN, R. W. and PARKER, C.F. 1967. Better pasture utilisation grazing cattle and sheep together. Ohio Reporter *57*, 12-13.

VICKERY, P.J. 1981. Pasture Growth Under Grazing.In Grazing Animals. Ed. F.H.W. Morley, World Animal Science, B1 Elsevier Scientific Publishing Company, Amsterdan-Oxford-New York. pp. 55-77.

VINE, D.A. 1977. Develppment of a pasture model for grazing studies. Ph. D. Thesis, University of Edinburgh.

WADE, M.H. 1979. Leaf and tiller dynamics in grazed swards. M Phil Thesis, Reading. 71p.

WARDLAW, I.F. 1969. The effects of water stress on translocation in relation to photosynthesis and growth. II. Effect during leaf development in *Lolium temulentum* L. Australian Journal of Biological Science *22*,1-16.

WARREN WILSON, J. 1963. Estimation of foliage denseness and foliage angle by inclined point quadrats. Australian Journal of Botany *11*, 95-105.

WELLS, G.J. 1974. The Biology of *Poa annua* and its significance in grassland. Herbage Abstract *44*, 385-391.

WHITE, J. and HARPER, J.L 1970. Correlated changes in plant size and number in plant populations. Journal of Ecology *58*, 467-485.

WILLIAMS, R.D. 1970. Tillering in grasses cut for conservation with special reference to perennial ryegrass. Herbage Abstract *40*, 383-388

WILLIAMS, C.N. and BIDDISCOMBE, E.F. 1965. Extension growth of grass tillers in the field. Australian Journal of Agricultural research *16*, 14-22.

WILLIAMS, R.F., EVANS, L.T. and LUDWIG, L.T. 1964. Estimation of leaf area for clover and Lucerne. Australian Journal of Agricultural Research *15*, 231-233.

WILLIAMS, C.H., DAVID, D.J. and IISMAA, O. 1962. The determination of chromic oxide in grass samples by atomic spectrophotometry. Journal of Agricultural Science, Cambridge *59*, 381-385.

WOLEDGE, J. 1978. The effect of shading during vegetative and reproductive growth of the photosynthetic capacity of leaves in grass sward. Annals of Botany *42*, 1085-1089.

WOLEDGE, J. and LEAFE, E.L. 1976. Single leaf and canopy photosynthesis in a ryegrass sward. Annals of Botany *40*, 773-783.

YODA, K., KIRA, T., OGAWA, H. and HOZUMI, K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. (Intra specific competition among the higher plants XI). Journal of Biology, Osaka City University *14*, 107-129.

APPENDIX A1

Table A1.1. Leaf lamina elongation rate (mm tiller^{-1}day^{-1}) of individual ryegrass tillers during 0-3 days before and 0-3, 3-6 and 6-13 days after defoliation. (Only the leaf in expansion at the moment of starting the experiment).

Treatment	0-3 days before	0-3 days after	3-6 days after	6-13 days after
T1 (50A)	8.1	3.7	1.0	0.3
T2 (50S)	8.2	5.4	1.2	0.6
T3 (100A)	7.2	4.2	1.1	0.2
T4 (100S)	7.3	5.3	1.5	0.2
T5 (100S+Sh)	7.3	3.3	0.8	0.3
T6 (100S+Sh)	9.1	4.5	1.8	0.3
T7 (C)	5.9	3.3	0.5	0.2
T8 (C)	8.1	3.6	0.8	0.3
$SE\bar{x}$	0.58	0.47	0.11	0.12

Table A1.2. Leaf lamina elongation rate (mm tiller^{-1}day^{-1}) of individual ryegrass tillers 0-3 days before and 0-3, 3-6 and 6-13 days after defoliation.

Treatment	0-3 days before	0-3 days after	3-6 days after	6-13 days after
T1 (50A)	10.2	8.2	4.5	3.8
T2 (50S)	9.8	8.8	3.5	3.9
T3 (100A)	9.7	8.1	4.5	2.9
T4 (100S)	9.0	8.7	4.5	3.4
T5 (100S+Sh)	9.5	8.3	4.3	2.8
T6 (100S+Sh)	10.5	6.9	3.6	3.0
T7 (C)	8.4	9.1	5.6	4.7
T8 (C)	10.6	8.9	5.7	4.4
$SE\bar{x}$	0.55	0.81	0.44	0.31

NO APPENDIX A2

APPENDIX A3

Table A3.1. Vertical distribution of the herbage mass (kg DM ha^{-1}) in swards continuously stocked, grazed by cattle or by sheep, from May to September 1980 (horizon depth 2 cm).

Treatments	H1+	H2	H3	H4	H5	H6*
SL	2000	100	0	0	0	0
SI	2700	410	80	10	0	0
CL	1800	80	0	0	0	0
CI	2500	430	70	10	0	0
CH	2100	770	390	250	170	260
$SE\bar{x}$	90.7	10.0	15.0	12.4	18.8	36.2

+Ground level to 2 cm horizon

*This horizon includes all mass above 10 cm height

Table A3.2. Height of the tips of the youngest and second youngest laminae (petiole) for ryegrass, *Poa* and white clover.

Period/Treatment	Height of the tip of the youngest leaf(mm)			Height of the tip of the second youngest leaf(mm)		
	Ryegrass	Poa	Clover	Ryegrass	Poa	Clover
SL	23.7	23.0	7.40	20.5	20.3	13.4
SI	39.4	28.9	11.10	33.8	24.5	22.4
CL	28.10	18.9	8.40	18.3	18.9	11.2
CI	41.50	26.8	8.90	39.2	32.3	16.6
CH	64.9	57.8	17.10	55.7	61.8	39.6
SL	27.0	21.4	11.3	20.6	21.1	15.6
SI	38.3	36.0	12.5	32.5	34.3	20.7
CL	33.4	28.8	9.3	24.6	29.5	19.6
CI	28.3	25.9	13.5	30.9	28.5	23.5
CH	53.0	51.8	17.2	61.3	51.0	32.1
SL	24.8	22.4	12.4	26.2	23.4	17.8
SI	28.6	32.1	17.6	25.4	26.2	18.8
CL	34.3	24.8	15.9	18.8	24.8	19.5
CI	38.1	24.9	11.8	28.8	30.2	25.6
CH	76.2	52.1	22.7	54.8	62.1	41.3
$SE\bar{x}$		3.28			3.75	

Table A3.3. Height of the ligule of the second youngest leaf and length of the pseudostem (stolon) for ryegrass, *Poa* and white clover.

Period/Treatment	Height of the ligule of the second youngest leaf (mm)			Lenght of the pseudostem (stolon) (mm)		
	Ryegrass	Poa	Clover	Ryegrass	Poa	Clover
SL	10.3	8.9	3.9	19.1	18.5	9.2
SI	15.2	15.4	6.4	23.8	18.8	13.7
CL	11.8	12.2	4.7	17.4	18.2	12.1
CI	18.1	14.9	1.5	19.0	25.5	13.2
CH	33.3	31.8	9.9	26.3	20.2	9.8
SL	14.0	11.3	3.4	20.3	17.7	16.5
SI	19.6	17.2	3.6	23.6	27.6	16.5
CL	13.5	13.6	5.2	19.0	25.5	13.2
CI	16.2	12.5	1.9	22.1	23.9	16.1
CH	23.9	25.0	3.6	35.1	33.7	26.0
SL	12.6	10.9	3.7	21.2	22.7	17.7
SI	16.1	16.4	8.2	22.2	25.3	16.4
CL	12.4	11.7	8.3	19.0	18.8	21.0
CI	17.6	15.0	5.5	20.2	20.9	14.8
CH	23.2	24.9	6.8	31.9	38.1	24.6
$SE\bar{x}$		2.20			2.11	

Table A3.4. Tiller/stolon angle to the ground (calculated as sine = length of pseudostem/stolon ÷ height of the ligule of the second youngest leaf for ryegrass, and *Poa* or height of the stipules of the younger leaf for clover).

Period/Treatment	Pseudostem Angle (degrees)		
	Ryegrass	Poa	Clover
SL	37.5	32.1	20.5
SI	47.1	54.9	39.5
CL	43.1	44.5	26.8
CI	52.2	47.6	5.6
CH	70.2	45.3	21.0
SL	45.0	46.0	13.2
SI	57.3	39.2	14.2
CL	46.6	35.3	21.2
CI	50.7	31.6	6.0
CH	44.6	49.1	7.2
SL	37.7	29.3	10.4
SI	47.7	41.3	33.3
CL	41.8	38.9	21.0
CI	60.2	45.3	22.3
CH	48.0	42.3	17.6
$SE\bar{x}$		4.05	

Table A3.5. Regression equations for lines in Figures E3.6 to E3.8 :. †

Tip of the youngest	RG+	10.30 ± 4.11 SSH°	+ 2.36 ± 4.185	R=0.93 *
	Poa	8.30 ± 0.94 SSH	+ 2.55 ± 3.560	R=0.92 *
	Clover	2.43 ± 0.52 SSH	+ 2.43 ± 1.962	R=0.77 *
2nd leaf	RG	9.55 ± 0.99 SSH	- 0.92 ± 3.725	R=0.93 *
	Poa	9.80 ± 0.89 SSH	- 0.98 ± 3.354	R=0.95 *
	Clover	6.02 ± 0.63 SSH	+ 1.30 ± 2.376	R=0.93 *
Ligule height	RG	4.86 ± (0.40) SSH	+ 0.63 ± 2.376	R=0.92 *
	Poa	4.26 ± (0.49) SSH	+ 1.10 ± 1.846	R=0.92 *
	Clover	0.59 ± (0.458) SSH	+ 3.02 ± 1.728	R=0.21 NS
Length of stem	RG	3.11 ± (0.523) SSH	+11.72 ± 1.971	R=0.84 *
	Poa	3.03 ± (0.853) SSH	+13.01 ± 3.215	R=0.67 *
	Clover	1.52 ± 0.874 SSH	+10.69 ± 3.295	R=0.36 NS
Angle	RG	19.96 ± 0.092 SSH	- 1.99 ± 1.080 $(SSH)^2$ + 6.582 ± 17.135	R=0.59 *
	Poa	1.98 ± 1.334 SSH	+37.5 ± 50.3	R=0.28 NS
	Clover	0.87 ± 1.95 SSH	+21.73 ± 7.35	R=0.12 NS

°SSH = sward surface height

+RG = Ryegrass

†n = 15 for all the equations

Table A3.6. Population density (units m^{-2}) for ryegrass and *Poa* tillers and active clover meristems, and for total active units.

Period	Treatment	Ryegrass	Poa	Clover	Total
June-July	SL	8000	16600	500	25100
	SI	7900	12250	1400	22900
	CL	5200	11600	30	16900
	CI	6100	10700	500	18000
	CH	9200	9600	1100	19900
mid-August	SL	17700	17100	200	34900
	SI	9900	14000	600	24700
	CL	12700	12900	900	25600
	CI	10800	10300	1500	24600
	CH	11600	7000	1800	20300
mid-Sept.	SL	13700	20100	700	34500
	SI	11400	15200	800	27400
	CL	8800	15400	1100	23000
	CI	6500	11700	900	21600
	CH	9600	8000	700	19300
April 1981	SL	8000	19200	100	27300
	SI	12400	17200	300	30000
	CL	4100	15900	500	20500
	CI	5000	18600	1200	25300
	CH	8300	6700	600	15600
	$SE_{\bar{x}}$	800	1000	300	2000

Table A3.7. Tiller appearance rate for ryegrass and *Poa* and active meristematic sites appearance rate for white clover (units.100 units^{-1}.day^{-1}).

Period/Treatment		Ryegrass	Poa	Clover
Period 1	SL	5.3	6.5	7.0
	SI	2.8	2.8	7.3
	CL	3.5	8.0	7.0
	CI	2.8	4.8	6.8
	CH	1.3	5.0	6.2
Period 2	SL	1.2	6.3	4.0
	SI	1.5	3.3	1.8
	CL	1.2	2.8	4.0
	CI	1.3	3.2	3.0
	CH	0.7	2.3	1.8
Period 3	SL	1.8	1.3	0.8
	SI	1.7	2.0	1.2
	CL	1.5	1.0	1.2
	CI	1.2	2.2	1.5
	CH	1.5	0.2	1.8
	$SE\bar{x}$			0.81

Table A3.8. Tiller disappearance rate for ryegrass and *Poa* and active meristematic sites disappearance rate for white clover (units.100 units^{-1}.day^{-1}).

Period	Treatment	Ryegrass	Poa	Clover
June-July	SL	1.3	2.5	6.2
	SI	1.0	2.5	1.8
	CL	4.8	5.5	6.0
	CI	2.3	3.5	1.8
	CH	2.0	0.3	1.8
mid-August	SL	1.5	2.3	3.7
	SI	0.2	2.8	1.2
	CL	1.7	2.2	4.2
	CI	2.0	1.0	2.0
	CH	0.3	1.2	0.5
mid-September	SL	0.3	0.2	0.3
	SI	0.2	0.7	0.3
	CL	2.5	1.3	0.8
	CI	0.8	1.3	0.5
	CH	1.7	1.8	0.3
	$SE\bar{x}$			0.80

Table A3.9. Tiller net change rate for ryegrass and *Poa* and active meristematic sites, net change rate for white clover (units.100 units^{-1}.day^{-1}) grazed.

Period	Treatments	Ryegrass	Poa	Clover
June-July	SL	4.0	4.0	0.8
	SI	1.8	0.3	5.5
	CL	-1.3	2.5	1.0
	CI	0.5	1.3	5.0
	CH	-0.7	4.7	4.3
mid-August	SL	-0.3	4.0	0.3
	SI	1.3	0.5	0.7
	CL	-0.5	0.7	-0.2
	CI	-0.7	2.2	1.0
	CH	0.3	1.2	1.3
mid-September	SL	1.5	1.2	0.5
	SI	1.5	1.3	0.8
	CL	-1.0	-0.3	0.3
	CI	0.3	0.8	1.0
	CH	-0.2	-0.7	1.5
	$SE_{\bar{x}}$			1.10

Table A3.10. Intervals between two defoliations for ryegrass, *Poa* and white clover (days).

Period	Treatments	Ryegrass	Poa	Clover
June-July	SL	5.7	13.5	8.4
	SI	8.2	15.0	7.8
	CL	7.8	9.9	7.8
	CI	8.2	14.1	6.9
	CH	7.7	10.2	6.9
mid-August	SL	5.0	9.2	6.8
	SI	6.2	14.0	7.6
	CL	6.5	8.3	7.0
	CI	9.4	11.5	7.0
	CH	12.0	15.7	9.7
mid-September	SL	8.9	8.9	12.5
	SI	10.2	8.4	8.5
	CL	8.9	18.7	7.8
	CI	10.8	12.3	15.3
	CH	10.2	13.5	9.0
	$SE_{\bar{x}}$			0.93

Table A3.11. Growth rate per primary unit for ryegrass, *Poa* and white clover ($\mu g.unit^{-1}.day^{-1}$) in continuously stocked swards grazed by cattle or by sheep from May to September 1980.

Period	Treatment	Ryegrass	Poa	Clover
June-July	SL	270.1	272.7	648.0
	SI	290.7	241.3	467.4
	CL	247.2	320.3	445.5
	CI	264.0	254.5	807.2
	CH	286.9	350.5	1091.8
mid-August	SL	196.6	223.5	601.6
	SI	688.1	287.7	873.0
	CL	266.5	210.0	750.6
	CI	361.7	398.5	1127.9
	CH	364.7	222.6	2139.3
mid-September	SL	257.8	180.9	61.7
	SI	329.9	182.5	403.9
	CL	225.8	160.9	1048.2
	CI	296.8	174.4	364.4
	CH	413.0	195.3	542.0
	$SE\bar{x}$			81.1

Table A3.12. Leaf senescence rate per primary unit for ryegrass, *Poa* and white clover ($\mu g.unit^{-1}.day^{-1}$) in continuously stocked swards grazed by cattle or by sheep from May to September 1980.

Period	Treatment	Ryegrass	Poa	Clover
June-July	SL	115.2	113.8	123.9
	SI	174.3	96.1	22.6
	CL	129.3	162.4	92.3
	CI	141.1	121.5	128.0
	CH	125.0	159.1	217.7
mid-August	SL	84.1	97.4	231.9
	SI	339.9	135.3	204.6
	CL	111.6	120.6	227.3
	CI	145.7	140.3	217.5
	CH	228.0	202.3	597.2
mid-September	SL	124.6	102.5	39.0
	SI	169.6	115.6	121.0
	CL	131.8	93.9	742.3
	CI	161.5	112.8	168.5
	CH	321.6	219.3	106.1
	$SE\bar{x}$			66.4

Table A3.13. Net growth per primary unit for ryegrass, *Poa* and white clover ($\mu g.unit^{-1}.day^{-1}$) in continuously stocked swards grazed by cattle or by sheep from May to September 1980.

Period	Treatment	Ryegrass	Poa	Clover
June-July	SL	115	159	524
	SI	116	145	445
	CL	118	158	353
	CI	123	133	679
	CH	162	191	874
mid-August	SL	112	126	370
	SI	348	152	668
	CL	155	89	523
	CI	216	258	910
	CH	137	20	1542
mid-September	SL	133	78	23
	SI	160	67	288
	CL	94	67	306
	CI	135	62	196
	CH	91	-24	436
	$SE\bar{x}$			66.4

Table A3.14. Growth rate ($kg.dm.ha^{-1}.day^{-1}$) for ryegrass, *Poa* and white clover in continuously stocked swards grazed by sheep or by cattle from May to September 1980.

Period	Treatment	Ryegrass	Poa	Clover
June-July	SL	15.4	27.9	2.0
	SI	17.6	25.0	4.9
	CL	12.4	21.1	0.1
	CI	16.2	25.4	3.7
	CH	29.8	28.1	12.7
mid-August	SL	31.3	31.5	0.8
	SI	62.6	38.1	3.8
	CL	24.4	24.7	5.8
	CI	41.4	37.6	14.1
	CH	41.6	16.1	24.5
mid-September	SL	31.0	31.9	0.4
	SI	33.3	24.2	2.5
	CL	13.9	21.8	11.9
	CI	26.8	18.2	3.0
	CH	36.0	14.3	3.2
	$SE\bar{x}$			5.10

Table A3.15. Leaf senescence rate ($kg.dm.ha^{-1}day^{-1}$) for ryegrass, *Poa* and white clover in continuously stocked swards grazed by sheep or by cattle from May to September 1980.

Period	Treatment	Ryegrass	Poa	Clover
June-July	SL	5.1	10.7	0.1
	SI	9.3	10.0	0.9
	CL	5.8	5.5	0.0
	CI	7.3	9.5	0.6
	CH	10.8	11.2	2.2
mid-August	SL	12.3	10.1	0.2
	SI	26.5	15.6	0.7
	CL	9.0	11.3	1.6
	CI	17.4	13.0	3.5
	CH	24.2	10.2	5.3
mid-September	SL	14.4	17.1	0.2
	SI	16.5	12.5	0.8
	CL	7.4	11.7	9.0
	CI	13.3	10.4	1.5
	CH	23.8	14.9	0.6
	$SE\bar{x}$			1.40

Table A3.16. Net production rate ($kg.dm.ha^{-1}.day^{-1}$) for ryegrass, *Poa* and white clover in continuously stocked swards grazed by sheep or cattle from May to September 1980.

Period	Treatment	Ryegrass	Poa	Clover
June-July	SL	10.3	17.3	1.9
	SI	8.3	15.1	3.9
	CL	6.6	11.6	0.1
	CI	8.8	15.9	3.1
	CH	19.0	17.0	10.6
mid-August	SL	19.0	21.4	0.6
	SI	36.0	22.5	3.1
	CL	15.4	13.3	4.2
	CI	24.1	24.6	10.6
	CH	17.3	5.9	19.2
mid-September	SL	16.6	14.8	0.1
	SI	16.8	11.7	1.6
	CL	6.5	10.1	3.0
	CI	13.5	7.8	1.5
	CH	12.3	-0.5	2.6
	$SE\bar{x}$			4.10

Table A3.17. Growth, senescence and net production rates (kg.dm. $ha^{-1}.day^{-1}$) in continuously stocked swards grazed by cattle (C) and by sheep (S) from May to September 1980.

Period	Treatment	Growth	Senescence	Net production
June-July	SL	45.4	15.8	29.5
	SI	47.5	20.1	27.3
	CL	33.6	15.3	18.3
	CI	45.3	17.5	27.8
	CH	70.7	24.1	46.5
mid-August	SL	63.6	22.6	40.9
	SI	104.5	42.9	61.6
	CL	54.9	21.9	33.0
	CI	93.1	33.8	59.3
	CH	82.2	39.7	42.4
mid-September	SL	63.3	31.7	31.6
	SI	60.0	29.8	30.2
	CL	47.7	28.1	19.6
	CI	47.9	25.1	22.8
	CH	53.6	39.2	14.4
$SE\bar{x}$ (n = 40)		4.6	2.2	3.7

Table A3.18. Major components of the diets of cattle and sheep determined visually from extrusa samples.

Period	Treatment	Total laminae	Total stem	Total dead	Roots
June-July	SL	0.83	0.10	0.04	0.03
	SI	0.82	0.15	0.02	0.01
	CL	0.64	0.18	0.08	0.08
	CI	0.67	0.22	0.05	0.06
	CH	0.64	0.28	0.06	0.02
August	SL	0.91	0.03	0.04	0.02
	SI	0.88	0.07	0.03	0.01
	CL	0.74	0.05	0.14	0.08
	CI	0.80	0.07	0.07	0.06
	CH	0.82	0.10	0.06	0.02
September	SL	0.91	0.02	0.03	0.05
	SI	0.84	0.06	0.04	0.04
	CL	0.85	0.03	0.04	0.07
	CI	0.80	0.06	0.07	0.08
	CH	0.86	0.07	0.04	0.03
$SE\bar{x}$		0.029	0.115	0.011	0.014

Table A3.19. Major components of the diets of cattle and sheep determined from extrusa samples with binocular help.

Period	Treatment	Ryegrass	Poa	Total†	Total stem	Total dead
June-July	SL	0.57	0.19	0.84	0.12	0.03
	SI	0.61	0.17	0.86	0.12	0.02
	CL	0.48	0.12	0.66	0.19	0.10
	CI	0.49	0.14	0.71	0.15	0.10
	CH	0.44	0.17	0.70	0.20	0.07
August	SL	0.41	0.27	0.70	0.16	0.07
	SI	0.46	0.20	0.72	0.15	0.09
	CL	0.57	0.10	0.75	0.06	0.14
	CI	0.50	0.19	0.69	0.12	0.15
	CH	0.64	0.09	0.75	0.15	0.09
September	SL	0.57	0.24	0.82	0.11	0.06
	SI	0.70	0.12	0.83	0.05	0.09
	CL	0.48	0.20	0.70	0.12	0.11
	CI	0.47	0.23	0.73	0.13	0.10
	CH	0.62	0.14	0.77	0.10	0.11
	$SE\bar{x}$	0.035	0.019	0.031	0.015	0.020

†The differences between total laminae and the sum of ryegrass and *Poa* is accounted for clover laminae.

Table A3.20. Live-weight gain for cattle (135 days), sheep (142 days) and lambs (105 days) calculated as the slope of the linear regression of weight on time ($kg.animal^{-1}.day^{-1}$)

Herbage Mass	Heifers	Ewes	Lambs
Low	0.100	-0.067	0.176
Intermediate	0.511	0.016	0.212
High	0.919		
$SE\bar{x}$	0.0722	0.0179	0.0196

APPENDIX A4

Table A4.1. Proportion of lamina leaf in areas covered by tall (A) and short (B) vegetation and average weighted for proportions (C).

		Animal species				
A	Herbage mass	C[+]	S	C+S	$\bar{x}$	$SE\bar{x}$
	1600	0.34	0.38	0.34	0.35	
	1900	0.46	0.39	0.37	0.41	0.022
	$\bar{x}$	0.40	0.38	0.35		
	$SE\bar{x}$			0.027		
B	1600	0.34	0.33	0.33	0.32	
	1900	0.36	0.35	0.38	0.36	0.015
	$\bar{x}$	0.34	0.35	0.34		
	$SE\bar{x}$			0.018		
C	1600	0.34	0.34	0.31	0.33	
	1900	0.39	0.37	0.38	0.38	0.009
	$\bar{x}$	0.34	0.37	0.36		
	$SE\bar{x}$			0.011		

[+]In all the Tables C = Cattle; S = Sheep; C+S = Cattle + Sheep

Table A4.2. Proportion of pseudostem in areas covered by tall (A) and short (B) vegetation and average weighted for proportions (C).

		Animal Species				
	Herbage mass	C	S	C+S	$\bar{x}$	$SE_{\bar{x}}$
A	1600	0.27	0.17	0.27	0.27	
	1900	0.22	0.18	0.15	0.20	0.008
	$\bar{x}$	0.25	0.18	0.21		
	$SE_{\bar{x}}$			0.010		
B	1600	0.16	0.22	0.18	0.19	
	1900	0.19	0.19	0.18	0.19	0.016
	$\bar{x}$	0.18	0.21	0.18		
	$SE_{\bar{x}}$			0.020		
C	1600	0.19	0.21	0.21	0.20	
	1900	0.20	0.19	0.17	0.19	0.013
	$\bar{x}$	0.20	0.20	0.19		
	$SE_{\bar{x}}$			0.015		

Table A4.3. Proportion of dead attached in areas covered by tall (A) and short (B) vegetation and average weighted for proportions (C).

		Animal species				
	Herbage mass	C	S	C+S	$\bar{x}$	$SE_{\bar{x}}$
A	1600	0.20	0.17	0.15	0.17	
	1900	0.14	0.20	0.14	0.16	0.011
	$\bar{x}$	0.14	0.17	0.18		
	$SE_{\bar{x}}$				0.013	
B	1600	0.21	0.15	0.19	0.18	
	1900	0.19	0.17	0.16	0.17	0.009
	$\bar{x}$	0.20	0.16	0.17		
	$SE_{\bar{x}}$			0.011		
C	1600	0.21	0.16	0.18	0.18	
	1900	0.17	0.18	0.15	0.17	0.007
	$\bar{x}$	0.19	0.17	0.17		
	$SE_{\bar{x}}$			0.009		

Table A4.4. Proportion of litter in areas covered by tall (A) and short (B) vegetation and average weighted for proportions (C).

		Animal species				
	Herbage mass	C	S	C+S	$\bar{x}$	$SE\bar{x}$
A	1600	0.11	0.21	0.13	0.16	
	1900	0.13	0.16	0.26	0.18	0.030
	$\bar{x}$	0.12	0.19	0.20		
	$SE\bar{x}$			0.034		
B	1600	0.19	0.21	0.23	0.21	
	1900	0.13	0.19	0.20	0.17	0.012
	$\bar{x}$	0.16	0.19	0.22		
	$SE\bar{x}$			0.015		
C	1600	0.21	0.17	0.21	0.20	
	1900	0.17	0.13	0.22	0.17	0.015
	$\bar{x}$	0.19	0.15	0.21		
	$SE\bar{x}$			0.019		

Table A4.5. Vertical distribution of the dry matter (proportion).

Horizon 0-2 cm from ground level.

Component	Lamina			Stem			Dead		
Animal sp.	C	S	C+S	C	S	C+S	C	S	C+S
Mass									
1600	0.26	0.29	0.40	0.18	0.21	0.18	0.19	0.16	0.17
1900	0.25	0.17	0.32	0.17	0.12	0.14	0.20	0.16	0.22
$SE_{\bar{x}}$			0.047			0.037			0.032
Horizon 2-4 cm									
1600	0.20	0.12	0.16	0.05	0.01	0.02	0.02	0.05	0.01
1900	0.22	0.30	0.18	0.04	0.02	0.01	0.04	0.06	0.04
$SE_{\bar{x}}$			0.030			0.017			0.020
Horizon 4-6 cm									
1600	0.07	0.06	0.04	0.01	0.01	0.01	0.01	0.00	0.01
1900	0.08	0.16	0.08	0.00	0.00	0.01	0.00	0.02	0.01
$SE_{\bar{x}}$			0.026			0.007			0.005

Table A4.6. Total and per species population densities in the areas covered by tall vegetation.

Period	Herbage mass	Animal sp.	Ryegrass	Poa	White Clover	Total
Sept.	1600	C	18500	3000	200	21600
		S	30600	7000	400	38000
		C+S	24100	4600	300	25400
	1900	C	21400	2000	200	23600
		S	21900	4900	400	27200
		C+S	24100	4900	700	29800
Oct.	1600	C	25900	6800	100	32700
		S	32700	1900	400	34900
		C+S	22600	4000	100	26700
	1900	C	18200	1000	400	19600
		S	18200	3400	100	21600
		C+S	18500	1300	200	20000
$SE_{\bar{x}}$			3700	2000	220	3700

Table A4.7. Total and per species population densities in the areas covered by short vegetation.

Period	Herbage mass	Animal sp.	Ryegrass	Poa	White Clover	Total
Sept.	1600	C	20800	2400	500	24200
		S	23900	3600	300	27800
		C+S	24400	2400	300	27100
	1900	C	24100	2300	600	26900
		S	24200	4900	400	29600
		C+S	24600	3600	400	28000
Oct.	1600	C	20100	2300	800	23200
		S	30200	2500	500	33200
		C+S	27500	4200	600	32300
	1900	C	18600	1900	1100	21500
		S	23900	3800	500	28100
		C+S	24600	2500	200	26200
$SE_{\bar{x}}$			1800	1000	230	2000

Table A4.8. Total and per species population densities weighted for proportion of area covered by tall and short vegetation.

Period	Herbage mass	Animal Sp.	Ryegrass	Poa	White Clover	Total
	1600	C	-	-	100	15400
		S	-	-	300	18500
June+		C+S	-	-	100	15900
	1900	C	-	-	1000	14300
		S	-	-	200	19800
		C+S	-	-	200	14600
	1600	C	20300	2900	400	23600
		S	25800	4500	300	30700
		C+S	23300	3000	300	26600
Sept.						
	1900	C	23300	2200	500	25900
		S	23100	4900	400	28400
		C+S	24500	3800	500	28900
	1600	C	21500	3300	600	25400
		S	30800	2400	500	33700
		C+S	26300	4100	500	30900
October						
	1900	C	18400	1600	900	20900
		S	21000	3600	300	24900
		C+S	22000	1400	200	23700
	1600	C	16200	6100	300	21900
		S	23170	4600	100	27300
		C+S	22330	6700	300	29100
May+						
	1900	C	17800	6600	400	24600
		S	20600	8700	200	28800
		C+S	20400	4400	300	25700
	$SE_{\bar{x}}$	a*	1900	1200	160	2200
		b	-	-	280	1800
		c	2000	1200	100	2000

+ random samplings

*a $SE_{\bar{x}}$ for all comparisons between means for September and October
b $SE_{\bar{x}}$ for all comparisons between means for June
c $SE_{\bar{x}}$ for all comparisons between means for May

Table A4.9. Appearance, disappearance and net change rates in ryegrass tillers estimated from cohorts of 20 tillers marked per week.

Herbage mass/Animal Sp.	Rate (tillers.100 tillers.day^{-1})								
	Appearance			Disappearance			Net change		
	C	S	C+S	C	S	C+S	C	S	C+S
1600	1.2	1.1	1.2	0.9	0.4	0.6	0.3	0.7	0.6
1900	0.9	1.4	2.3	0.3	0.6	0.3	0.5	0.8	2.0
$SE\bar{x}$			0.40			0.23			0.27

Table A4.10. Appearance, disappearance and net change rates in ryegrass tillers calculated from individual tillers during 3 (1) and 8 (2) weeks after marking.

1.

Herbage mass/Animal sp.	Rate (tillers.100 tillers day^{-1})								
	Appearance			Disappearance			Net change		
	C	S	C+S	C	S	C+S	C	S	C+S
1600	1.7	5.5	1.4	1.4	0.2	0.5	0.2	5.2	0.9
1900	2.9	2.6	1.9	0.2	0.0	0.5	2.6	2.6	1.4
$SE\bar{x}$			1.0			0.2			1.0

2.

1600	1.6	4.2	2.2	1.3	0.5	0.9	0.3	3.8	1.3
1900	2.2	2.1	1.5	0.5	0.4	0.4	1.5	1.9	1.2
$Se\bar{x}$			0.70			0.30			0.7

Table A4.11. Rate of appearance, disappearance and net change of ryegrass (a), Poa (b) tillers and white clover active meristems (c) used in tissue turnover.

a.

Rate (tillers.100 tillers day^{-1})

Herbage mass/Animal sp.	Appearance			Disappearance			Net change		
	C	S	C+S	C	S	C+S	C	S	C+S
1600	5.8	6.9	7.2	1.1	0.6	4.7	4.7	6.4	2.5
1900	5.0	4.4	2.8	2.8	0.0	0.8	2.2	4.4	1.9
$SE\bar{x}$			1.4			1.65			2.10

b.

Rate (tillers.100 $tillers^{-1} day^{-1}$)

Herbage mass/Animal sp.	Appearance			Disappearance			Net change		
	C	S	C+S	C	S	C+S	C	S	C+S
1600	8.3	13.1	8.3	3.6	5.8	9.7	4.7	7.2	1.4
1900	14.2	11.7	11.7	3.1	2.5	0.6	11.1	9.2	11.1
$SE\bar{x}$	1.40			1.65			2.10		

c.

Rate (active meristem.100 $a.m.^{-1} day^{-1}$)

Herbage mass/Animal sp.	Appearance			Disappearance			Net change		
	C	S	C+S	C	S	C+S	C	S	C+S
1600	3.9	4.4	4.7	1.4	0.3	1.7	2.5	4.1	3.1
1900	3.6	2.8	2.2	0.0	0.3	0.0	3.6	2.5	2.2
$SE\bar{x}$		1.40			1.65			2.10	

Table A4.12. Interval between defoliations (days) for ryegrass, Poa and white clover in tall (a) and short (b) pats.

HM/Plant sp. / Animal sp.	Ryegrass			Poa			White clover		
	C	S	C+S	C	S	C+S	C	S	C+S
a) Tall									
1600	10.3	4.8	7.0	8.3	4.4	5.6	19.1	4.8	19.1
1900	7.5	17.3	11.0	5.9	5.6	5.6	6.7	17.3	2.8
$SE\bar{x}$									2.4
b) Short									
1600	6.0	7.4	8.1	8.2	8.1	5.8	6.7	8.8	6.7
1900	7.7	10.3	5.6	6.8	6.9	8.02	9.3	8.7	7.9
$SE\bar{x}$									1.70

Table A4.13. Growth, senescence, and net growth rates per primary ryegrass tillers (μg dm $tiller^{-1}day^{-1}$) in areas covered by tall (A) and short (B) vegetation and weighted for proportions of both (C).

A. Rate (μg dm $tiller^{-1}day^{-1}$)

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	759	417	629	176	119	346	583	298	284
1900	433	826	698	269	357	483	165	469	215
$SE\bar{x}$			91.0			45.4			122.1

B. Rate (μg dm $tiller^{-1}day^{-1}$)

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	248	219	286	84	66	77	164	153	209
1900	354	335	420	80	93	101	274	272	319
$SE\bar{x}$	a^+		27.1			10.2			22.5
	b^+		33.2			12.5			27.6

C. Rate (μg dm $tiller^{-1}day^{-1}$)

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	360	247	397	106	81	148	254	166	249
1900	380	492	512	139	222	244	241	270	268
$SE\bar{x}$			66.8			21.0			70.6

$^+$ for all the following tables when only one $SE\bar{x}$ is given it is for comparison of means between the body of the table otherwise a = $SE\bar{x}$ for comparisons between levels of mass, and b = $SE\bar{x}$ for comparison between animal species.

Table A4.14. Gross growth, senescence and net growth rates per primary Poa tillers in areas covered by tall (A), short (B) vegetation and weighted for proportions of both (C).

A.

Rate (μg dm $tiller^{-1} day^{-1}$)

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	265	308	210	203	148	58	62	160	153
1900	300	459	267	181	180	84	120	279	183
$SE\bar{x}$			91.0			45.5			122.1

B.

Rate (μg dm $tiller^{-1} day^{-1}$)

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	176	230	286	100	88	76	77	142	79
1900	310	232	379	131	70	138	180	162	241
$SE\bar{x}$	a[+]		27.1			10.2			22.5
	b		23.2			12.5			27.6

C.

Rate (μg dm $tiller^{-1} day^{-1}$)

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	200	261	166	125	104	72	75	157	94
1900	317	329	394	146	124	115	171	206	279
$SE\bar{x}$			66.8			21.0		a	27.1
								b	33.2

[+] See Table A4.13.

Table A4.15. Gro growth, senescence and net growth rates per primary clover active meristem (μg dm tiller^{-1}day^{-1}) in areas covered by tall (A), short (B) vegetation and weights for proportion of both (C).

A. Rate (μg dm active meristem^{-1} day^{-1})

	Gross growth			Senescence			Net growth		
HM/Animal sp.	C	S	C+S	C	S	C+S	C	S	C+S
1600	1374	446	368	84	36	55	1290	410	313
1900	1154	742	951	281	97	47	1058	461	905
$SE\bar{x}$			91.0			45.4			122.1

B. Rate (μg dm active meristem^{-1}day^{-1})

	Gross growth			Senescence			Net growth		
HM/Animal sp.	C	S	C+S	C	S	C+S	C	S	C+S
1600	345	290	191	52	53	51	292	237	141
1900	493	435	425	170	89	101	323	346	324
$SE\bar{x}$	a[+]		27.1			10.2			22.5
	b		33.2			12.5			27.6

C. Rate (μg dm active meristem^{-1}day^{-1})

	Gross growth			Senescence			Net growth		
HM/Rate Animal sp.	C	S	C+S	C	S	C+S	C	S	C+S
1600	591	339	238	60	48	52	531	291	186
1900	709	593	616	147	182	82	562	411	534
$SE\bar{x}$			66.8			21.0		a	27.1
								b	33.2

[+] See Table A4.13.

Table A4.16. Growth, senescence and net growth per unit area (kg dm ha^{-1} day^{-1}) for ryegrass in the areas covered by tall (A) and short (B) vegetation and weighted for proportion of both (C).

A.

Rate (kg dm $ha^{-1}day^{-1}$)

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	127.2	115.7	115.4	25.4	32.3	48.3	101.8	83.4	67.1
1900	75.9	170.4	160.5	56.5	71.6	101.7	19.4	98.8	58.8
$SE\bar{x}$			14.1			8.5			a[+] 6.4
									b 7.8

B.

Rate (kg dm $ha^{-1}day^{-1}$)

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	41.3	52.7	55.9	10.0	13.0	12.0	31.3	39.7	43.9
1900	69.2	68.3	101.8	14.0	15.5	20.4	55.2	52.8	81.4
$SE\bar{x}$			4.1			1.1			4.1

C.

Rate (kg dm $ha^{-1}day^{-1}$)

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	62.7	61.1	75.4	14.1	18.7	22.3	48.6	42.4	53.0
1900	71.3	103.3	121.5	27.1	42.9	51.3	44.2	60.4	70.2
$SE\bar{x}$			5.2			3.0			a 4.2
									b 5.1

[+] See Table A4.13.

Table A4.17. Growth, senescence and net growth per unit area (kg dm $ha^{-1}day^{-1}$) for Poa in the areas covered by tall (A), short (B) vegetation and weighted for proportions of both (C).

A.

Rate (kg dm $ha^{-1}day^{-1}$)

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	8.5	19.3	5.5	3.7	10.0	1.2	4.8	9.2	4.3
1900	6.2	21.9	7.6	4.6	6.4	2.0	1.6	15.5	5.6
$SE\bar{x}$			14.1			8.5		a[+]	6.4
								b	7.8

B.

Rate (kg dm ha^{-1} day^{-1})

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	3.9	5.2	1.9	1.4	1.2	0.8	2.4	3.9	1.2
1900	4.4	6.5	8.2	1.6	1.6	2.3	2.8	4.9	5.9
$SE\bar{x}$			4.1			1.1			4.1

C.

Rate (kg dm ha^{-1} day^{-1})

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	5.1	9.9	2.8	2.3	3.7	0.9	2.8	6.2	2.0
1900	5.2	13.5	9.4	2.4	3.9	2.1	2.7	9.5	7.4
$SE\bar{x}$			5.2			3.0		a	4.3
								b	5.1

[+] See Table A4.13.

Table A4.18. Growth, senescence and net growth per unit area (kg dm $ha^{-1}day^{-1}$) for white clover in the areas covered by tall (A), short (B) vegetation and weighted for proportions of both (C).

A.

Rate (kg dm ha^{-1} day^{-1})

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	2.3	1.5	1.0	0.1	0.1	0.2	2.2	1.4	0.8
1900	2.5	2.2	1.5	0.2	0.6	0.1	2.3	1.6	1.4
$SE\bar{x}$			14.1			8.5		a[+]	6.4
								b	7.8

B.

Rate (kg dm ha^{-1} day^{-1})

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	1.2	0.5	0.7	0.3	0.1	0.1	0.9	0.4	0.6
1900	2.8	1.8	1.6	1.0	0.2	0.3	1.8	1.5	1.3
$SE\bar{x}$			4.1			1.1			4.1

C.

Rate (kg dm ha^{-1} day^{-1})

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net growth C	Net growth S	Net growth C+S
1600	1.4	1.0	0.9	0.1	0.1	0.2	1.3	0.9	0.7
1900	2.5	1.9	2.0	0.5	0.4	0.3	2.0	1.5	1.7
$SE\bar{x}$			5.2			3.0		a	4.2
								b	5.1

[+] See Table A4.13.

Table A4.19. Growth, senescence and net production per unit area (kg dm $ha^{-1}day^{-1}$) for combined species in areas covered by tall (A), short (B) and weighted for proportions of both (C).

A.

Rate (kg dm ha^{-1} day^{-1})

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net production C	Net production S	Net production C+S
1600	138	136	122	29	43	50	108	94	72
1900	85	195	170	79	61	104	24	116	66
$SE\bar{x}$			15.8		a[+]	9.1			19.2
					b	11.1			23.5

B.

Rate (kg dm ha^{-1} day^{-1})

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net production C	Net production S	Net production C+S
1600	46.4	58.4	58.5	12.0	14.2	13.4	34.4	44.2	45.2
1900	76.4	76.6	111.6	16.2	17.4	23.0	60.2	59.2	88.6
$SE\bar{x}$	a		8.3			2.1			8.4
	b		102.			2.6			10.3

C.

Rate (kg dm ha^{-1} day^{-1})

HM/Animal sp.	Growth C	Growth S	Growth C+S	Senescence C	Senescence S	Senescence C+S	Net production C	Net production S	Net production C+S
1600	70.1	78.4	77.2	16.5	22.5	23.4	53.6	55.9	53.8
1900	78.7	134.5	135.9	30.0	47.2	53.6	48.7	87.3	82.3
$SE\bar{x}$	a		10.9			2.0			12.6
	b		11.7			2.5			15.5

[+] See Table A4.13.